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A Quarterly Journal of Research and Technical Progress

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Distribution of Rainfall Under Forest Stands

BY
G. K. VOIGT

IN ANY GIVEN STORM the distribution of rainfall on even a relatively small area is often subject to considerable variation due to such meteorological factors as storm intensity and wind velocity. Superimposed on these vagaries of the atmosphere are the effects of vegetation cover which may be particularly pronounced in forested regions. Rain falling on a forest canopy may be intercepted, or it may reach the forest floor directly through holes in the canopy as "throughfall." Some of the intercepted water is recycled to the atmosphere by evaporation. The remainder is absorbed by the crowns or is concentrated by the foliage, branches and trunks and reaches the soil as drip, or as "stemflow."

The proportion of each of these components in relation to total precipitation has been recorded for a number of conditions (Hamilton and Rowe, 1949; Hoover, 1953; Ovington, 1954; and Rowe and Hendrix, 1951). The earlier literature has been summarized by Kittredge (1948). Such studies indicate that the effect of a canopy varies with storm intensity and that interception ranges from 100 percent in short light showers to as low as ten percent in heavy rains.

It also appears that the relative role of stemflow is of minor importance, generally, ranging from 1 to about 15 percent depending on storm characteristics, species and canopy characteristics. From the standpoint of microclimatology, however, the latter values are misleading because they are based on the assumption that the water flowing down the stem of an individual tree is spread uniformly over the projected crown area of that particular tree. In reality this is not the case; only a relatively narrow band around the base of the tree is affected by stemflow. This redistribution of rainwater is of great importance to the moisture economy of trees (Hoover, 1953) as is indicated by studies of root distribution (Stout, 1956). In addition, it undoubtedly has hydrologic implications since such a mechanism is an effective means of recharging subsoil moisture. This paper reports the results of a study of the distribution of rainfall under forest stands with particular reference to stemflow.

Methods and Materials

The study area was located in southern Connecticut about eight miles east of New Haven. This area receives about 45 inches of precipitation per year, chiefly as rain. Observations were made over a two-year period.

During the first growing season, the relationship between soil moisture and rainfall was observed under three eastern hemlock (*Tsuga canadensis* [L.]Carr.) and three red pine (*Pinus resinosa* Ait.) canopies using Colman fiberglas resistance units. All

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trees were growing on a sandy loam soil. Under each tree, units were placed at soil depths of one, three, nine and 24 inches at four positions along a radius from the stem to the crown projection line. The first stack of units was placed one foot from the stem of the tree and remaining stacks were placed at successive one-foot intervals outward. In addition, units were placed three inches from the stem of each tree at depths of one and nine inches. The effects of 13 storms during the period from May through September were determined by periodic resistance measurements. Measurements were taken daily from May through August and as soon as possible after each storm in September. The results of these observations formed the basis for interpreting the quantitative aspects of stemflow recorded in the second portion of the study.

Twentieth-acre plots were laid out in three types of forest cover—red pine, hemlock, and American beech (*Fagus grandifolia* Ehrh.)—and in an open area. The red pine plot was located in a 35-year-old plantation that had been thinned to about 500 trees per acre; at the time of the study the canopy was 85 percent closed. The trees had an average d.b.h. of eight inches and an average height of 50 feet. The lower branches of red pine are approximately perpendicular to the main stem whereas the smaller branches near the top form an acute angle. The bark is scaly with the lower portion of the large flat scales often curving away from the stem.

The hemlock plot was located in a hemlock-hardwood mixture with hemlock comprising about 70 percent of the stand. When the hardwoods were in leaf the canopy was about 90 percent closed. The hemlock trees selected for stemflow measurements occupied dominant and codominant positions in the stand and had an average d.b.h. of 9.5 inches and an average height of 55 feet. Hemlock exhibits an excurrent form, the lower branches being nearly perpendicular to the central axis. The smaller branches at the upper end of the crown tend to extend upward to form an acute angle with the stem. The bark is deeply furrowed on the lower stem but is smooth near the top.

The beech plot was located in a nearly pure stand of beech with individuals in all stages of development. The trees selected for stemflow measurements were dominants and codominants with an average d.b.h. of six inches and an average height of 52 feet. The crowns of the trees overlapped considerably and when the trees were in foliage the canopy was 100 percent closed. The lateral branches of beech form an acute angle with the main axis. The bark of the branches and the main stem is very smooth.

The open plot was located in the center of a half-acre clearing created by logging an old hemlock stand. The vegetation was chiefly herbaceous with scattered hemlock seedlings. The opening was surrounded by young hardwoods and hemlocks which graded into the older forest.

The plots were laid out in a relatively straight line in the following order: red pine, hemlock, beech and open. The distance from the red pine plot to the open plot was about 1200 feet.

Rain gauges were constructed by soldering 12-inch sections of galvanized stove pipe eight inches in diameter to galvanized eight-inch funnels. Each gauge rested on the upper end of a 24-inch section of eight-inch stove pipe driven into the ground. The rain water was caught in a gallon jug inside the supporting stove pipe.

The collars for intercepting stemflow were made from semicircles of appropriate diameter cut from sheet aluminum. The aluminum was drawn up tight against a gasket of fiberglas insulation glued to the tree. The aluminum was fastened with tape to form a collar. The joint between the tree and the aluminum collar was made watertight by impregnating the gasket with Log Sealer, SB-525, manufactured by the Angier Adhesives Company, 120 Potter Street, Cambridge, Mass. Tygon tubing was sealed into a hole drilled in the bottom of the collar to carry the water to tared

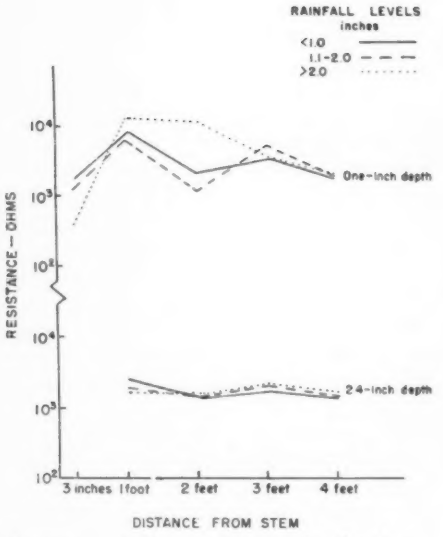

FIGURE 1. *Resistance changes of soil moisture units under a hemlock canopy for storms of three size classes.*

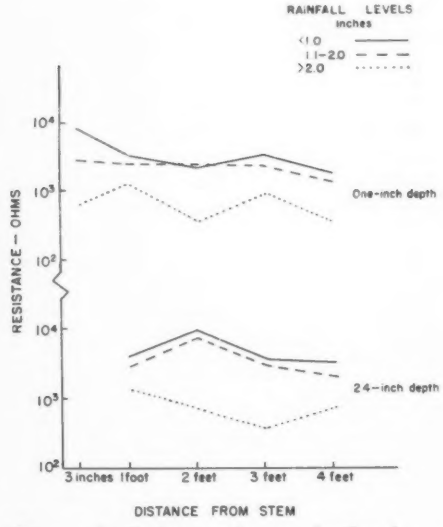

FIGURE 2. *Resistance changes of soil-moisture units under a red pine canopy for storms of three size classes.*

five-gallon cans connected in tandem. The amount of stemflow was determined by weighing the cans and their contents immediately after each storm.

Stemflow measurements were made on seven trees in each forest cover type. Trees were selected to represent the range of diameters on each plot. Throughfall and drip were measured by five rain gauges on each forested plot. The gauges were placed in the form of a grid and their positions changed three times during the course of the study. Total rainfall for each storm was measured by five gauges on the open plot. These values generally showed good agreement with the data collected by a U. S. Weather Bureau station four miles from the study area. Interception was determined by difference.

Bark texture was investigated by measuring water recovery from a ten-foot segment of one stem of each tree species. A perforated collar was placed ten feet above a regular stemflow collar and water was added to the upper collar in increments of one liter. The water was allowed to flow for 15 minutes after it had been added and the amount from each increment recovered in the collecting vessel of the lower collar was measured.

Stemflow characteristics of a ten-foot segment of red pine were observed by using collars of different sizes. The collar sizes were determined by measuring the horizontal distance from the edge of the collar to the tree stem. This distance was varied from 19 inches to one inch. All observations were made on the same tree during a single, sunny, calm day. The recovery technique previously described was used.

Results and Discussion

The behavior of the soil-moisture resistance units indicated irregular rainfall distribution under the forest canopy. It was observed that precipitation was concentrated in certain spots by dripping from the ends of branch stubs and leaves, or direct fall through holes in the canopy. Although this erratic distribution made it difficult to draw

any concrete conclusions relating to large areas, certain patterns were evident. Typical results are shown in Figures 1 and 2. Thirteen storms have been arranged in three groups to eliminate some of the variability exhibited by individual storms of low intensity. There were eight storms totaling less than one inch, four between 1.1 and two inches, and one greater than two inches.

The curves for the resistance units under the hemlock tree at the one-inch depth (Fig. 1) show that the distribution of moisture in the soil resulting from rainfall was quite variable according to the distance from the stem. The depression in the curves for the two lower rainfall levels at the two-foot position are due to the fact that the stack of moisture units happened to be placed directly under a branch stub that funneled water flowing down the branch onto the units. Therefore, the units were almost always in wet soil when readings were taken.

With this exception, the pattern of soil moisture from current precipitation under a hemlock canopy was what one might expect. The values for units placed three inches from the stem reflected the water flowing down the stem into the soil. Those at the one-foot position showed relatively higher resistance values indicating the intercepting effect of the crown. This trend continued at the three-foot position. At the four-foot position the effect of the crown was diminished and drip from the edge of the crown lowered the resistance values of the units here. The most clear-cut illustration of canopy effect is shown by the curve for the single storm greater than two inches. The reason for the lack of the depression shown by the other two storm classes at the two-foot position is not obvious. It may have been the result of wind blowing the drip from the branch stub and distributing the water more generally rather than concentrating it directly onto the stack of soil moisture units in the soil profile.

The unts placed at the 24-inch depth at the various positions showed a remarkable similarity for all storm classes indicating the greater stability of soil moisture at this increased depth.

Figure 2 shows resistance values for the units at the same positions for the same storms under the canopy of a red pine tree. In this case, redistribution by the canopy was much less apparent. The more open nature of the stand allowed greater amounts of water to penetrate the canopy and infiltrate the soil. With the possible exception of the storm having greater than two inches of precipitation there was no appreciable influence of stemflow on soil moisture. The values at the 24-inch level were less uniform and the soil somewhat drier than in the hemlock plot. This is probably due to the more open nature of the red pine stand in comparison with the hemlock. Increased air movement and greater penetration of sunlight probably caused higher evaporation losses which were transmitted to the lower soil depths. The single storm greater than two inches showed more vertical penetration under red pine than it did under hemlock. This reflects the lower intercepting capacity of the red pine crown in comparison with hemlock.

When one considers the overall results of the study of soil moisture distribution under tree canopies as shown by soil moisture units, it must be borne in mind that the true relationship between resistance values and rainfall for any particular storm may be masked by soil moisture from a previous storm. Only after a sufficient period of dry weather may the true effect of rainfall on soil moisture be observed.

This is illustrated by the curves for both plots for the single storm greater than two inches. The storm occurred on September 7, 1956, after about three weeks of dry weather during which the soil moisture level was depleted by active evapo-transpiration. The dry condition of the soil permitted the close canopy of the hemlock and the more open one of red pine to be reflected by the resistance values shown for this storm. Individual storms occurring in close sequence are less likely to be accurately recorded than individual storms occurring

at longer intervals. This factor must be taken into account if soil moisture units are to be used in evaluating the effect of individual rain storms on the distribution of soil moisture.

The results also indicate the difficulty of obtaining a detailed picture of the distribution of rainfall as indicated by soil moisture. The reasons for this are: localized concentrations of stemflow, drip from branch stubs and from the edges of crown canopies, and direct penetration of rain through openings in the crown located more or less at random over the forest floor. It is evident that such variations are of considerable significance when one is attempting to describe the soil moisture regime in any one stand either from a silvicultural or a hydrologic point of view.

In two storms resistance values indicated that the water flowing down the tree stems had some tendency to follow the root channels into the soil. Attempts were made to reproduce this pattern by causing water to flow down beech stems and observing the advance of the wetting front in the soil.

Colman fiberglas resistance units were placed in the surface soil at distances of five and ten inches from the tree. Some units were inserted as close to large roots as possible and others were placed between the large roots. Movement of water in the soil was determined by noting the resistance of the units before and after water was made to flow down the stem. These attempts were generally unsuccessful because of local variations in soil or microtopography.

On two occasions, however, the pattern referred to earlier was observed. Results of one of these trials indicate more rapid movement of water in soil surrounding large roots than in the soil between large roots (Table 1). This phenomenon has important hydrologic implications, since several investigators have found that the role of roots and root channels in downward movement of water through the soil profile is of appreciable significance.

Hursh and Hoover (1941) indicated that the annual decay of roots each year and their subsequent channeling by microorganisms and small insects create relatively large continuous openings that serve as pathways for rapid movement of water. Gaiser (1952a) found the number of vertical channels to exceed 4,000 per acre. He concluded that it was likely that vertical channels are interconnected by lateral channels formed in a similar way. Because the channels are relatively more permeable to water than the surrounding soil, he concluded that the channels could serve as pathways for the rapid movement of a large part of the free water in a soil profile. Gaiser states, "In view of these observations it is highly probable that estimates of the physical and hydrologic characteristics of soil will be

TABLE 1. Movement of the wetting front in soil near a beech stem after 5 gallons of water were made to flow down the stem. Water was added over a 10-minute period. Values are resistance of Colman soil-moisture units in ohms.

Location of resistance units	Time in relation to water addition (minutes)				
	−10	+10	+30	+60	+90
Next to root—5 inches from tree	6.5×10^3	6.1×10^2	6.1×10^2	6.1×10^2	7.0×10^2
Between roots—5 inches from tree	1.4×10^4	1.2×10^4	1.3×10^4	7.2×10^2	7.2×10^2
Next to root—10 inches from tree	1.1×10^4	1.1×10^4	1.1×10^4	7.2×10^2	7.2×10^2
Between roots—10 inches from tree	9.5×10^3	9.5×10^3	9.5×10^3	9.5×10^3	8.7×10^2

TABLE 2. Redistribution of rainfall by canopies of three forest cover types. Values are averages based on 13.4 inches of rainfall.

Cover type	Interception		Throughfall		Stemflow projected crown area		Stemflow absorption area	
	inches	*percent*	*inches*	*percent*	*inches*	*percent*	*inches*	*percent*
Red pine	2.5	18.7	10.7	80.1	0.1	1.2	1.6	12.1
Hemlock	4.4	33.1	8.1	60.9	0.8	5.9	12.7	94.8
Beech	3.3	24.7	8.8	65.7	1.3	9.6	37.0	276.0

seriously in error unless some allowance is made for the discontinuities in the soil profile resulting from decay of taproots and their laterals." Gaiser (1952b) also noted that soil taken from the vicinity of root channels was wetter than the surrounding soil. The pattern of wetting appeared to be one of expanding pockets within the horizon rather than blanket wetting from above.

These observations emphasize the hydrologic importance of the network of root channels for transporting water vertically and horizontally through forest soils. It may well be that stemflow serves as a principal point of entry to this network since living roots often occupy old root canals (Lutz and Chandler, 1946, p. 255).

The quantitative aspects of rainfall distribution under three cover types are shown in Table 2 and Figure 3. These data, collected during the period from May to October 1957, represent observations made on 21 storms totaling 13.4 inches. The values for interception, throughfall and stemflow are in general agreement with those recorded by previous investigators. It should be pointed out that the value for throughfall is composed of the water which fell unimpeded through holes in the canopy plus the water which filtered down through the canopy and reached the forest floor as drip. In several instances, gauges located under drip-release positions indicated higher values than were recorded by the gauges in the open. Similar findings have been reported by Ovington (1954) and Wicht (1941).

Of particular interest are the values for stemflow. When these values were calculated on the basis of the crown-projection area, they constituted a relatively small percentage of the total rainfall. The study of the previous growing season, however, indicated that the water flowing down the stem was, in fact, not distributed over the

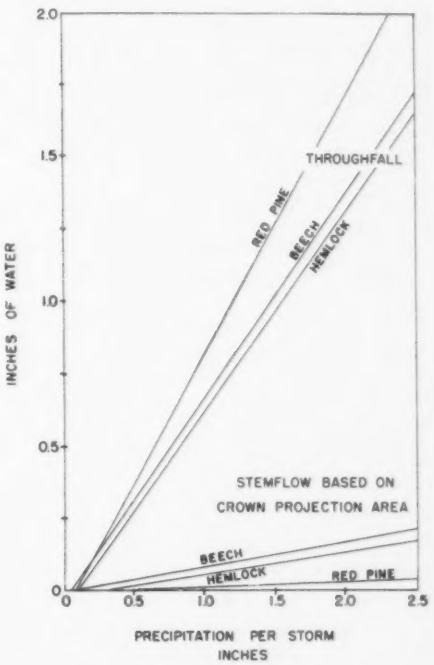

FIGURE 3. *Throughfall and stemflow based on crown projection area under three cover types in relation to storm intensity.*

entire crown-projection area but was limited to a rather restricted area closely adjoining the stem of the tree. In most cases, this absorption area for stemflow had a radius of less than one foot from the circumference of the tree. When the calculations were made using the annular area with a one-foot radius (Table 2), the values assumed a much more important role in the total hydrologic picture of the forest stand. The stemflow values for beech exceeded those for the other two species considerably. During the entire season, the amount of water received from stemflow on the absorption area in the beech stand was over two and one-half times greater than the rainfall in the open. In the hemlock stand the amount was about equal to rainfall in the open and in red pine it was about one-fifth of the value for the open. The relationships for individual storms are shown in Figure 4.

There are a number of factors that may regulate the magnitude of stemflow. Those peculiar to the cover type include such aspects as branching habit of the species, form and texture of the leaves, and bark texture. The effect of bark texture is

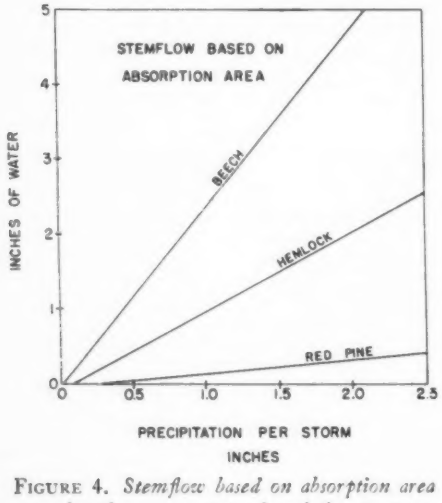

FIGURE 4. *Stemflow based on absorption area under three cover types in relation to storm intensity.*

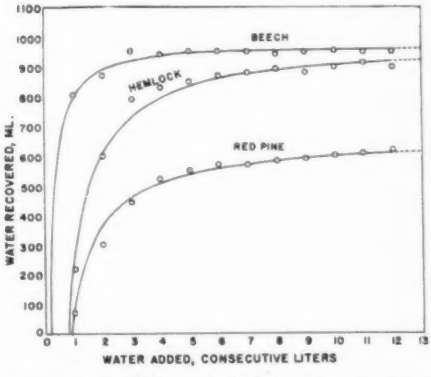

FIGURE 5. *Effect of bark texture on water recovery from 10-foot segments of stems of three species.*

shown in Figure 5. These curves partially explain the results observed over the growing season. It is evident that of the three species, beech with its smooth bark allowed the most complete and rapid recovery of the water which flowed down the stem. Nearly all water was recovered from each increment after the addition of the fourth liter. From this point on the slope of the curve remains approximately the same (Fig. 5). With hemlock the slope increases gradually and is still increasing after the addition of the twelfth liter, nearly attaining the value observed for beech. The curve for red pine, on the other hand, indicates a much lower recovery value and although the slope was slightly upward, it was separated from the total for beech by 300 milliliters.

These variations in recovery are probably due in part to differences in total surface on the stems of the three species. It appears that beech bark has a relatively low storage capacity whereas red pine is capable of retaining relatively large quantities of water. Such differences would be especially significant in storms of low intensity and short duration.

There is another factor involved in the case of red pine. While the observations on bark texture were being made, it was apparent that part of the water that started to flow down the red pine stem dripped off

the edges of the curled bark plates. This suggests that the water was falling in a diffuse pattern around the stem rather than flowing along the outer surface. Thus where narrow collars are used to intercept stemflow, low values for this component result. An indication of the magnitude of this zone of stem fall may be obtained from Figure 6. This curve shows that the water in the zone of stem fall was distributed rather uniformly from the surface of the tree outward for at least 19 inches. Although these observations were limited to red pine it is likely that other species with rough bark behave similarly.

The overall results of the study emphasize the role of stemflow in the hydrologic aspects of watershed areas or in relation to the water economy of forest stands and individual trees. Since much water is concentered in a relatively small zone around the stem of each tree, it undoubtedly allows greater vertical penetration of the soil and thus serves to recharge the sub-surface layers. This, of course, affects the total water economy of individual trees by enabling them to make more efficient use of each increment of rainfall.

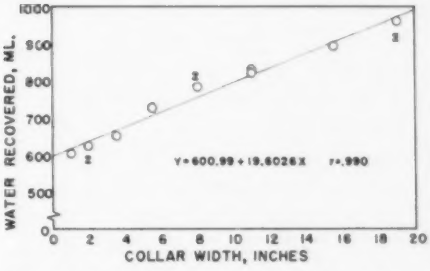

FIGURE 6. *Effect of collar width on water recovery from a 10-foot segment of a red-pine stem.*

Summary

Rainfall distribution patterns under forest covers of red pine, hemlock, and beech were investigated. Soil moisture observations showed that a considerable portion of the water which fell on the canopy was concentrated by the foliage, branches and stem, and eventually released to the soil in a relatively narrow band around the base of the tree. There were indications that the water flowing down the stem tended to follow the larger roots into the soil. When the magnitude of stemflow was calculated on the basis of the absorption area, it was found that the soil at the base of the average red pine tree received about one-fifth of the amount which fell in the open, soil under hemlock received the same amount of rainfall as the open area, and soil under beech received about two and one-half times the amount falling on the open area. Water recovery values from trunk segments of the three species indicated that bark texture may offer a partial explanation for the stemflow differences. Red pine bark absorbed considerably more water than beech. Further observations on red pine indicated that much of the water concentrated by the foliage and branches fell in a diffuse zone around the stem rather than flowing down the outer bark surface. Presumably this was due to the curled bark plates that caused the water to drop rather than flow.

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Nitrogen Metabolism in Plants

By George C. Webster. 152 pp., illus. Row, Peterson and Company, Evanston, Ill., 1959, $3.50.

Review by H. A. Fowells
U.S. Forest Service, Washington D. C.

Research is adding new knowledge at such a rate that only a few can keep up with original literature in any one specialty. This is particularly true in biochemistry. The author of this monograph has brought together current ideas and research in a limited field of plant biochemistry, namely, the metabolism of nitrogen. Specifically the author has confined his review to four phases of nitrogen metabolism: nitrogen nutrition, amino acid metabolism, biosynthesis of amides and peptides, and protein and nucleic acid metabolism. Higher plants obtain their nitrogen from three sources: nitrate, ammonia, or amino acids. Once absorbed by the plant, nitrate is reduced to ammonia which in turn combines with organic acids to form amino acids. There is some evidence that ammonia is not formed but the pathway proceeds through a combination of hydroxylamine with an α-keto acid to an α-amino acid.

However formed, the amino acids are the principal first products of nitrogen assimilation. Although the amino acids are the building blocks of protein, many do not combine into protein but exist as intermediates in the formation of other amino acids, growth regulators, alkaloids, and other nitrogenous substances. The author presents step by step pathways for many of these transformations.

The plant amides, such as glutamine and asparigine, and peptides, among which are some vitamins, are common nitrogenous compounds in plants. The biosynthesis of these compounds proceeds via a system of enzymatic reactions. For the amides ammonia is added to an amino acid and for the peptides two or a few more amino acids are joined in peptide linkage. The formation of these simple peptide bonds provides an insight for the formation of the bonds in the complex protein molecule.

Synthesis of the hundreds of different plant proteins from the same 18 or 20 amino acids requires a control in the plant cell of unbelievable specificity. For a particular protein the evidence is that all the individual amino acids are needed at the same time, that energy is required for the synthesis, and that nucleic acid also must be present, possibly as the "mastermind," directing the enzymatic transformation.

This monograph would not be easy reading for many foresters. But it will accomplish what the author intends it to do—provide information on current progress for research workers outside this particular field, education for new workers in the field, and a basis for reexaminations of ideas for those already in the field.

Distribution of Slash Pine as Related To Certain Climatic Factors

BY
JAMES E. BETHUNE

THE CONCEPT THAT CLIMATE determines the geographic distribution of vegetation is generally accepted among ecologists. Seasonal variations in temperature and rainfall are considered the most important climatic factors limiting the geographic distribution of a given species (Daubenmire, 1956).

Because of its rapid growth and value for timber and naval stores, slash pine (*Pinus elliottii* Engelm.) is one of the most important commercial tree species in the southern pine region. Most of the seedlings planted in reforestation programs in the South are slash pine (Mergen, 1955).

The natural range of the species extends from southern South Carolina westward through the Atlantic and Gulf Coastal Plains to eastern Louisiana, and southward to the Gulf of Mexico and central Florida. Seed source and racial studies indicate that slash pine is susceptible to variations in climatic conditions even within its natural range, but the species has been successfully grown in some areas outside of, but adjacent to, its natural range (Hebb, 1955).

Hocker (1956) found that average temperature and the frequency and intensity of precipitation during the summer were the most important climatic factors, of those he studied, associated with the distribution of loblolly pine (*Pinus taeda* L.). His findings indicated some localities where loblolly pine apparently could safely be planted outside the natural range. The usefulness of this knowledge prompted a similar study of the climatic factors associated with the natural distribution of slash pine.

Procedure

The degree to which climatic factors are associated with the occurrence of slash pine can be determined by a comparison of the values of these factors inside the range with similar values outside the range. A technique which permits the simultaneous comparison of a number of factors, and takes into account any correlations among them, is the discriminant function method of analysis (Cox and Martin, 1937). This method makes use of multiple regression to yield an equation in terms of those factors that differ most widely between specified groups of the dependent variable relative to their variation within these groups. Thus, the equation can be used to classify any single observation into the proper group on the basis of the values of the significant factors.

In this instance the groups are selected stations inside and outside the natural range of slash pine (Fig. 1). The factors selected were governed by the climatological records available. Average temperature, range of temperature, and length of the frost free period were chosen as the temperature factors likely to prove of value in discriminating between the two regions. Similarly, average precipitation and frequency of precipitation were selected. Frequency was divided into frequency of precipitation of

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0.01 inch or greater and frequency of precipitation of 0.50 inch or greater. The latter expression is probably a better measure of effective precipitation. An equation of the following form was fitted to these data:

$$Y = a + b_1x_1 + b_2x_2 \ldots b_{21}x_{21}$$

in which

$Y = +1$ for stations inside slash pine range and -1 for stations outside the range.

x_1 to x_4 = average monthly temperature in winter, spring, summer, and autumn, respectively, in degrees F.

x_5 to x_8 = average monthly range of temperature in winter, spring, summer, and autumn, respectively, in degrees F.

x_9 to x_{12} = average monthly frequency of days with precipitation of 0.01 inch or more in winter, spring, summer, and autumn, respectively.

x_{13} to x_{16} = average monthly frequency of days with precipitation of 0.50 inch or more in winter, spring, summer, and autumn, respectively.

x_{17} to x_{20} = average monthly precipitation in inches in winter, spring, summer, and autumn, respectively.

x_{21} = average length in days of the frost-free period.

$a, b_1, b_2, \ldots b_{21}$ = constant and coefficients derived from the data.

The seasonal averages were obtained by computing the arithmetic averages of 3-month periods from 30-year monthly averages compiled by Hocker (1955). Winter includes December through February; spring, March through May; summer, June through August; and autumn, September through November. These averages were computed for 23 stations inside the range of slash pine and 27 stations in the territory adjacent to and approximately equal in area to the range (Fig. 1).

[1]Because the number of stations inside the range was less than the number outside, the initial value of the constant, a, had to be adjusted by adding to it one-half the difference between the two calculated mean discriminants of the two regions, to make them equidistant from zero.

The normal equations were solved progressively, the variables being segregated in descending order of their contributions to the sum of squares of deviations from the mean of the dependent variable.

Results

The analysis produced the following regression equation (Table 1).[1]

$$Y = -1.325 - 0.2923\ (x_{12}) - 1.2586\ (x_{13}) + 1.6593\ (x_{14}) + 0.5661\ (x_{15})$$

in which

Y = the calculated discriminant value.

x_{12} = average monthly frequency of precipitation of 0.01 inch or more in *fall*.

x_{13} = average monthly frequency of precipitation of 0.50 inch or more in *winter*.

x_{14} = average monthly frequency of precipitation of 0.50 inch or more in *spring*.

x_{15} = average monthly frequency of precipitation of 0.50 inch or more in *summer*.

The accuracy of a discriminant function may be expressed by the probability of misclassification. This probability is determined by the normal deviate of the regression equation, which is computed by dividing half the difference between the two regional mean discriminants by the standard deviation of a single observation, or:

$$\text{Mean deviate} = \frac{\frac{1}{2}\ (0.8147)}{0.8089} = 0.5036$$

According to the table of normal deviates (Pearson, 1930), a deviate of 0.5036 indicates a probability of misclassification of 31 percent. Thus the chance of correctly classifying a randomly selected station is about two out of three.[2]

[2]The elimination of significant variables may introduce a positive bias into the absolute value of the difference between the two mean values of the discriminant function, and a negative bias into the standard deviation. Thus, the probability of misclassification may be underestimated.

The calculated discriminant values for each station (Fig. 1) resulted in the misclassification of three stations inside the range and five stations outside the range. Actual misclassification therefore was 16 percent, or somewhat less than expected.

Because a plus value for the calculated discriminant indicates a similarity in climate to that of the slash pine region, and a minus value indicates a dissimilarity, a line following the zero discriminant value should separate the two regions (Fig. 1).

Discussion

The climatic factors found to be significant between the natural range of slash pine and the area immediately outside its range are expressions of the seasonal frequency and intensity of precipitation.

The significance of these variables does not, however, establish them as factors limiting the distribution of the species. For example, in the Southeast summer rainfall increases toward the south and east; thus, averages of summer rainfall on either side of any line roughly parallel to the coast would differ significantly if the averages were based on areas of sufficient size.

The largest difference in rainfall frequency occurs in summer, when heavy rains occur on 4.05 days per month inside the range and 3.35 days per month in the adjoining region (Fig. 2). This difference is about 20 percent of the frequency outside

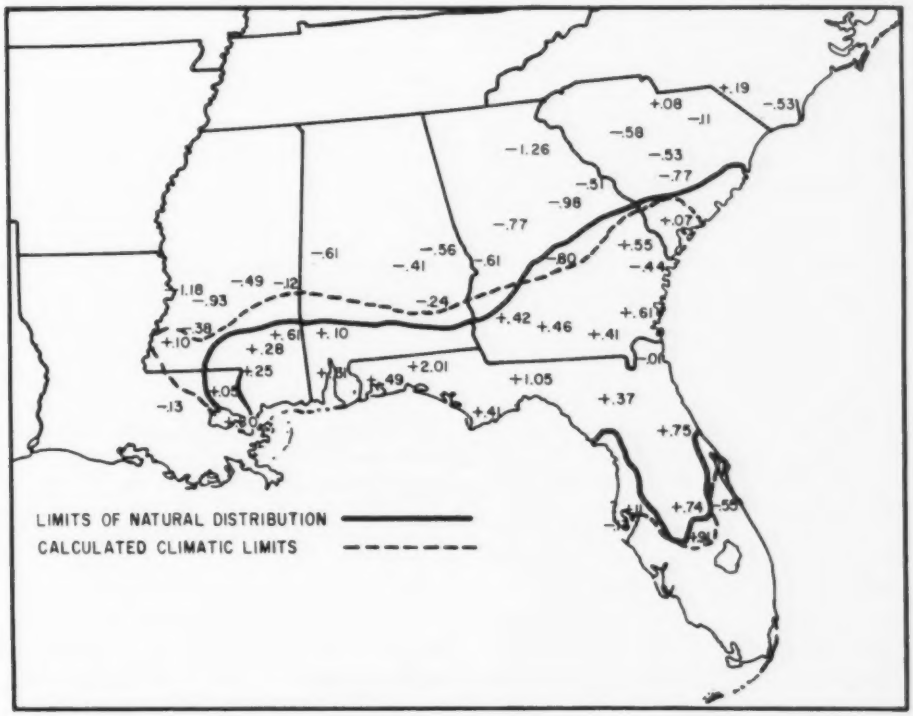

FIGURE 1. *Map showing the calculated discriminant values for the 50 climatological stations, the limits of natural distribution of slash pine, and the calculated climatic limits.*

the range and represents for the season an amount of rainfall that is greater than the difference in total summer precipitation between the two regions (Table 2). Because soil moisture is replenished much more effectively by heavy than by light rains (Shreve, 1914), the substantial difference in frequency of heavy rains during a large part of the growing season could be an important factor in the occurrence of the species. Low frequency of summer rains would affect first-year seedling survival. That the observed difference is enough to preclude seedling establishment seems doubtful, but as one of several critical factors it could be important. Plant distribution is often limited by failure of the reproductive phase, and in southern pines inadequate soil moisture during the growing season may limit the formation of flower buds (Wenger, 1957) and retard the development of cones and seed (Wakeley, 1954).

The second largest difference in rainfall frequency occurs in winter when heavy rains are more frequent in the adjoining area than in the slash pine range. Although not in itself significant, this variable ap-

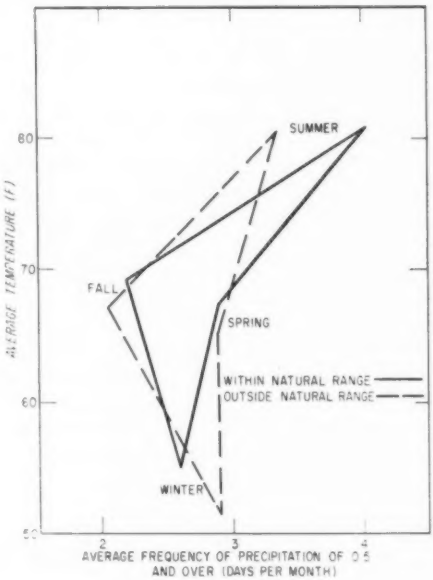

FIGURE 2. *Average temperature and average frequency of precipitation for the area within the natural range of slash pine and the area immediately without the range.*

TABLE 1. Analysis of variance for the discriminant function showing average seasonal values for the significant variables (variables listed in order removed).

Source of variation	D.F.	Sum of squares	Mean square	F	Seasonal averages (in days) Within	Outside	In-out
x_{15} Average monthly frequency of precipitation $\leq$ 0.50 inch, summer	1	11.2331	11.2331	15.25**	4.05	3.35	+0.70
x_{14} Average monthly frequency of precipitation $\leq$ 0.50 inch, spring	1	3.8200	3.8200	5.19*	2.91	2.87	+0.04
x_{13} Average monthly frequency of precipitation $\leq$ 0.50 inch, winter	1	1.9793	1.9793	2.69	2.60	2.91	−0.31
	} 2	5.2110	2.6055	3.54*			
x_{12} Average monthly frequency of precipitation $\leq$ 0.01 inch, fall	1	3.2317	3.2317	4.39*	7.28	7.10	+0.18
Other variables	17	8.7972	0.5175				
Residuals	28	20.6187	0.7364				
Mean	1	0.3200	0.3200				
Total	50	50.0000					

**Significant at the 1 percent level.
*Significant at the 5 percent level.

TABLE 2. Average seasonal precipitation and average frequency of precipitation inside and immediately outside the range of slash pine.

Season	Average precipitation		Average frequency of precipitation 0.5 inch	
	Inside	Outside	Inside	Outside
	Inches		*Days per month*	
Winter	11.7	12.3	2.60	2.91
Spring	13.2	12.9	2.91	2.89
Summer	18.6	15.6	4.05	3.35
Fall	11.1	9.9	2.18	2.08

parently is associated with the frequency of autumn rainfall, x_{12}, since the latter becomes significant only after the effect of winter differences is segregated. Because of the lower level of life processes during the dormant season, this difference probably is not very important in the occurrence of slash pine. The northern boundary of the species range is well to the south of regular snowfall, although glaze storms occasionally occur. Heavier rains in late winter can inhibit or prevent pollination; thus, the more frequent heavy winter rains in the adjoining territory could be an additional limiting factor.

Differences in frequency of rains in spring and fall, although significant, are quite small. In the spring, heavy rains occur on 0.04 more days per month inside the range than outside. In the fall the difference in frequency of heavy rains is not significant, but light rains occur on 0.18 more days per month inside the range than in the adjacent area. Because these differences are so small, it seems unlikely that they have a real effect on the occurrence of the species.

The failure of average monthly temperatures and monthly temperature ranges to be significant is probably because they do not adequately express temperature variations between the two areas. Average minimum, yearly minimum, and periodic minimum temperatures are likely more important in limiting the distribution of a species. Cold periods following warm periods in late winter and early spring frequently kill trees; consequently, their number and duration might limit the distribution of a species. It has also been shown recently that the difference in day and night temperatures has a significant effect on growth of loblolly pine seedlings (Kramer, 1957); closely related species such as slash pine might be similarly affected. Unfortunately the lack of data precluded an analysis of these factors.

It is realized that parent material and soil formation are also correlated to a very high extent with species distribution. Local site conditions and site-climatic interactions can and do overshadow climatic effects and may account for some of the deviation between the limits of natural distribution and the calculated climatic limits in Figure 1.

The conclusion is that analysis of climatic factors by means of the discriminant function will show which factors are associated with the distribution of a species. This information may be useful in indicating where the species might be planted outside its natural range. However, significant association of climatic variables with species occurrence does not show how they operate to limit the distribution of the species. The greatest value of discriminant-function analysis probably lies, therefore, in its usefulness in planning further research, because it shows where additional work is likely to be most profitable.

The line following the calculated zero discriminant value closely parallels the line of actual distribution of slash pine. Many areas in South Carolina, Georgia, Alabama, Mississippi, Louisiana, and east Texas, which are adjacent to the natural range of slash pine, may lack sufficient precipitation during the growing season for optimum development of the species. Slash pine is now being planted in many of these areas, but plantations are for the most part too young to provide satisfactory data on growth rates throughout the period of a rotation. Scattered reports of stagnation, slowing of

growth, and failure to express dominance in plantations from sapling to pole size may possibly be attributed to insufficient summer rainfall. Before deciding to plant slash pine in these localities, the alternative of planting species of southern pine native to the region should be considered. In central Florida the calculated distribution line extends farther south than does the line of natural distribution used in this study, although in general they are parallel.

Regions outside the natural range of slash pine which proved to have climatic conditions significantly similar to the natural slash pine area are small zones in South Carolina, southern Mississippi, and western Louisiana. Slash pine should prove a valuable species for planting within these zones on suitable sites. The results of this study suggest, however, that the planting of slash pine outside its natural range should be undertaken with caution, and only after careful consideration of all local climatic variations and specific site conditions.

Summary

The relationship of climatic variables to the natural distribution of slash pine was studied. The variables used were monthly averages of temperature and precipitation by seasons, and average length of the frost-free period, for 23 stations within the range of natural distribution of slash pine and 27 stations in the area outside of, but adjacent to, its range.

The data were analyzed by the discriminant function method. The following variables, listed in the order selected, were found to be significant in discriminating between the two regions:

Average monthly frequency of precipitation ≧0.50 inch, summer
Average monthly frequency of precipitation ≧0.50 inch, spring
Average monthly frequency of precipitation ≧0.50 inch, winter[3]
Average monthly frequency of precipitation ≧0.01 inch, autumn

[3]Significant in combination with the fourth variable removed.

The analysis does not establish these variables as limiting factors to the growth of slash pine. Further study is needed to determine how these climatic differences may operate to affect the occurrence of the species.

When the regression equation is applied to individual stations, a plus value for Y indicates climatic conditions similar to those in which slash pine grows naturally, and a minus value indicates dissimilar conditions. On a map showing the weather stations a line tracing the zero (Y) values should, therefore, separate the two regions. This line parallels closely the boundary of natural distribution of the species (Fig. 1).

Areas of South Carolina, Georgia, Alabama, Mississippi, and Louisiana which are outside but adjacent to the northern limit of natural distribution of slash pine appear suitable climatically for the species. Other areas in these same states that are farther removed from the zone of natural distribution, but where slash pine is presently being planted, may lack sufficient frequency of heavy rains. Planting in these areas should be undertaken with caution and with careful consideration of the site requirements and silvical characteristics of the species.

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Forests and Streamflow

Der Einfluss des Waldes und des Kahlschlages auf den Abflussvorgang, den Wasserhaushalt und den Bodenabtrag. (The influence of forests and clearcut areas on streamflow, the hydrologic process and erosion.) Results of the first 5 years of a forest-hydrological study in the Oberharz (1948-1953); and one separate appendix of tables with 105 pages. By Delfs, J. et al. 1958. M. and H. Schaper, Hannover, Germany. 223 pages. No price indicated.

Review by B. H. Heede
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The German Forest Service as well as the German public were concerned about the forest area clearcut during World War II and the immediate post war years. Heavy erosion damage that would permanently endanger the growth of trees was expected. Therefore, in 1948 the Forest Service of Lower Saxony began a study of runoff and erosion in the Upper Harz Mountains. Two experimental watersheds were chosen. One had been clearcut and was 186 acres in size. The other was forested with pure Norway spruce (*Picea abies*) and had an area of 215 acres. In 1950 and 1951 respectively, 2 additional watersheds, each with a complete cover of Norway spruce and areas of 80 to 95 acres, were added for replication. The flow of two springs was measured to estimate base flow and to determine trends during wet and dry periods.

The climate favored vegetation. After 5 years it was found that natural establishment and growth of vegetation prevented serious erosion. Mean annual temperature was 42.5° F, mean precipitation yielded 53.11 inches, and 84 percent was the mean relative humidity. Native vegetation covered nearly all of the clearcut watershed by 1955. Gully erosion below a logging skid trail, 910 feet long with a drainage area of 0.7 acre, amounted to 180 cu ft in 1949 and decreased to zero in 1955. Sheet erosion from 9 ft x 3 ft plots on bare mineral soil totaled 8.01 tons/acre/year, but dropped to only 0.15 ton/acre/year after establishment of a vegetal cover (*Aira flexuosa*).

The influence of the vegetation on erosion was investigated by measurement of suspended sediment of streams. The method used gives indices only. Samples were collected in milk bottles installed in an upright position and without a separate air outlet. The bottles were protected by mesh wire cages which may also have prevented collection of representative samples. During the first two years the suspended sediment load of the untreated watershed amounted to only 29 percent of that of the clearcut watershed. Larger differences existed in bed load and coarse sediment transport. In 1949, 61.1 cu ft were deposited at the gaging station of the clearcut drainage as compared with 2.5 cu ft from the forested

area. Beginning in 1953 with the natural regrowth of the vegetation, the treated watershed contributed no coarse sediment.

It is regrettable that there were no measurements before the watershed was clearcut. Therefore, the study does not permit definite comparison of the clearcut watershed with the forested watershed. The mean daily flow for the forested and clearcut areas is so similar (2.05 cfs/sq mi and 1.97 cfs/sq mi respectively) that differences between them could be within the measuring error. A comparison of the instantaneous maximum flow of the watersheds shows a more pronounced discrepancy (forested watershed: 19.89 cfs/sq mi; clearcut watershed: 25.48 cfs/sq mi).

Intensive studies of interception by a forest canopy were executed under Norway spruce stands of different age classes. Extra large rainfall pans (16.5 ft x .66 ft) were installed, each having an area equivalent to 50 standard rain gages (Hellman type). The installation of a large rainfall collector eliminates the weakness of older German studies that used only a few rain gages. However, it is doubtful that the few large rain pans improved sampling sufficiently to permit extrapolation of the results. This is unfortunate because it is unusual for a study of interception by a forest canopy to continue for 4½ uninterrupted years.

This publication contains detailed descriptions of climate, topography, geology, soils, vegetation, and hydrologic aspects of the experimental watersheds. Since it is planned to continue the study for another 5 years, it would be desirable—after all the effort and expense—to clearcut one of the replicated watersheds. Only then changes in the hydrologic regimen can be related to treatment. Yet, the investigation demonstrated that there was no serious erosion problem so long as natural revegetation takes place. The study is a valuable contribution to our knowledge about watersheds.

Forest Machinery

By E. R. Huggard and T. H. Owen, Albert and Charles Black Ltd., London, 192 pages, 123 illustrations. 1959. 24s.

Review by A. N. Foulger
The University of Michigan, Ann Arbor

During the many years devoted to afforestation in Great Britain attention has centered on the development of mechanization in nursery and site preparation work. Now, as large areas of plantations have grown into the thinning stage, increasing interest is being shown in the applicability of machines to protection, felling, and extraction. Firms throughout the country have engaged in the production of various mechanical implements and it has become increasingly difficult for the forester to know what is available to meet his particular needs. The authors have made a real contribution to British forestry by placing in this single volume a large amount of information concerning the existence and use of a multiplicity of machines.

Though this book will be of primary importance in Great Britain, readers in North America will find in it much of interest and application under certain conditions. The first three chapters discuss the place of machines in forestry generally, and the economic and organizational questions posed by mechanized operations. Subsequent chapters deal with types of mechanical equipment presently used in a particular phase of forest management, e.g. road construction, site preparation, extraction. Most of the units referred to are of British manufacture but many have American counterparts. The tables of machine and work specifications are of equal application on either side of the Atlantic. The differing conditions are most apparent in the section on forest fire protection. Here reference is restricted to the use of pumps and portable water tanks with no mention of plows, back-firing torches, and other mechanical devices which have been developed in the United States.

American foresters undoubtedly can read this text with considerable profit. Various applications of machinery in the forest are presented lucidly and with many excellent illustrations. The numerous tables should make the book a most useful source of reference not only for the tyro but for the practiced forester.

Initiation and Ontogeny of the Ovulate Strobilus in Ponderosa Pine

BY
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N. T. MIROV

DESPITE THE LARGE volume of accumulated information for *Pinus*, only a meager amount of data is available on the time and mode of initiation of strobili or cones in the genus. Information on date of initiation and subsequent maturation of cones is of utmost importance to forest geneticists and foresters who are concerned with problems of hybridization and natural seed production.

In one study Allen (1941) called attention to the value of being able to identify cones in an early state of development for forecasting seed crops in conifers. He pointed out that Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forms ovulate cones on easily identifiable subterminal axes and that from this information a fair estimate of next season's cones can be made. By counting buds on many sample branches a "cone intensity" ratio—the ratio between the number of ovulate buds and the number of vegetative buds for a given tree—can be established. The initial estimate must, of course, be modified later to account for subsequent insect damage, cone abortion, and adverse climatic conditions.

Recognition of young ovulate strobili is relatively easy if the conelets are not initially enclosed by terminal bud scales. This is true of Douglas-fir, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), true firs (*Abies* spp.) and western redcedar (*Thuja plicata* Donn) (Allen, 1941). In the genus *Pinus*, the cones are lateral in position but their early development occurs within the scales of the well protected terminal bud. The terminal bud itself continues to grow vegetatively after cones appear in the spring. External evidence of cones may not become apparent until late winter or even early spring, after the conelets have grown considerably. Admittedly, measurements of terminal buds and close attention to "cone patterns" of previous years enable the observer to make a fair estimate of the presence of ovulate cone primordia. However, early accurate estimates can only be established by carefully performed dissections.

There are some reports in the literature regarding the date of cone initiation for several species of *Pinus*. These are summarized in Table 1. The present paper is concerned with megasporangiate or ovulate

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TABLE 1. Date of cone initiation for certain species of Pinus.

Author and date of publication	Geographical location	Species[1]	Date of cone initiation: Megasporangiate or ovulate	Date of cone initiation: Microsporangiate
Strasburger, E., 1872 (data from Mergen and Koerting, 1957)		*P. pumilio*	late August	early August
Ferguson, M. C., 1904	Mass., U.S.A.	*P. strobus*	not found as late as Nov. 20	not found in fall
		P. rigida	ditto	Oct. or Nov.
		P. austriaca	ditto	Oct. or Nov.
Coulter, J. M. & C. J. Chamberlain, 1910	Chicago, Ill., U.S.A.	*P. laricio*	late fall and winter	not reported
Doak, C. C., 1935	from widely separated regions of U.S.A. and neighboring islands	7 species	mid August	end of July
Little, E. L. Jr., 1938	Flagstaff, Ariz., U.S.A.	*P. edulis*	August-Sept.	August-Sept.
Mergen, F. and L. E. Koerting, 1957	Lake City, Florida, U.S.A.	*P. elliottii*	late August	mid July
Wareing, P. F., 1958	Oakmere, Cheshire, England	*P. sylvestris*		
		1951—Tree 1	August 22	August 10
		1951—Tree 3	September 12	no data
		1952—Tree 1	August 14	August 1

[1]Specific names are those used by original authors.

cone initiation and development for ponderosa pine (*Pinus ponderosa* Laws.). It also includes, in the tabular summary, information from the literature on microsporangiate strobili.

Materials and Methods

Material for this study was obtained from 65-year-old ponderosa pine trees growing on the grounds of the Institute of Forest Genetics, Placerville, California, altitude 3,000 feet. Collections were made at intervals from September 1957 through September 1958. Terminal buds which presumably would contain ovulate strobili were collected from the crowns of trees, whereas potentially microsporangiate buds were collected from lower branches. The distribution pattern of potentially fertile shoots in older trees is fairly well established for pines and has been described in detail by Wareing (1958) for *P. sylvestris* L.

The terminal buds collected in summer and fall were dissected and the outer refractory bud scales removed. Strobili that could be identified were killed and fixed individually. Most of the material was fixed in aqueous chromic acid-propionic acid-formalin solutions. The principal formulations were those of Randolph (1935) and Sass (1951, Craf III). Butanol was employed as the dehydrating and clearing agent. The schedule followed was that of Brooks, *et al.* (1950). Sectioned material was stained with tannic acid-iron chloride and counterstained with safranin according

to the schedule of Foster (1934). In addition to safranin, fast green was employed as a counterstain.

Observations

September 18, 1957. By this date growth in length of a main vegetative branch had ceased for the year and a terminal bud had formed. This consisted of a "telescoped" system of appendages and branches, *viz.*, basal bud scales, spur-shoot primordia (future leaf fasicles) and ovulate cone primordia (each subtended by a scale), and a group of scales which overarched the apex. After removal of the larger bud scales the young ovulate or megasporangiate strobili present could be identified rather easily. The cone primordia (usually three or four in number) and the main vegetative shoot tip were excised and preserved separately for future examination.

Topographically the vegetative shoot was dome shaped (Fig. 1). The cytological zonation pattern at that time was essentially that described for *Pinus ponderosa* by Sacher (1954), *viz.*, a centrally located group of larger, vacuolate cells (central mother cell zone), surrounded peripherally by a zone of smaller, deeply staining cells (peripheral zone), and a basal zone of cells (rib meristem) which give rise to the future pith. The cells of the latter zone are frequently in distinct longitudinal rows when the shoot is rapidly elongating; at this stage of development the regularity of these cell lineages was somewhat obscure.

With careful manipulation an ovulate cone primordium could be excised as described above, the scales around the cone removed, and the entire cone photographed (Fig. 2). A cone primordium on September 18, 1957 was approximately 300 μ wide at the base and 125 μ high. Prior to the date of collection the apical meristem of the young cone [which had its origin as an axillary bud, comparable to that of a dwarf or short vegetative shoot (leaf fasicle)] had given rise to scales which overarched the apex. Subsequently the apical meristem and its meristematic derivatives produced the conical mound of tissue (young cone) which was without appendages (Fig. 5).

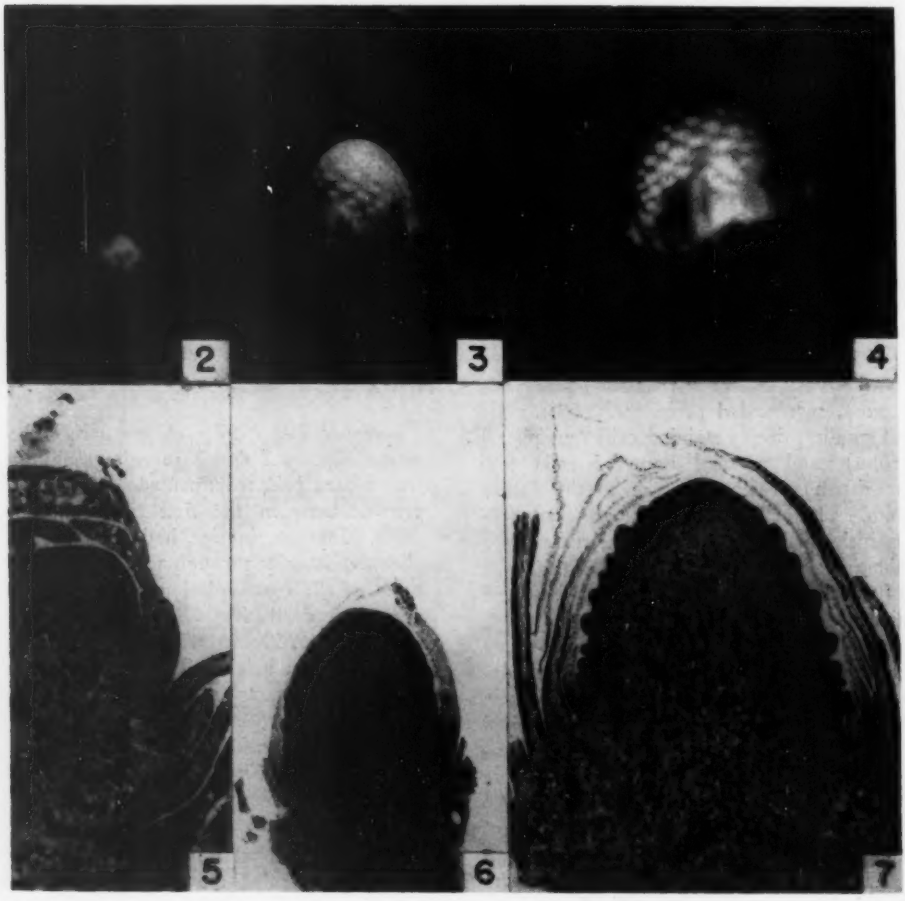
FIGURE 1. *Median longitudinal section of vegetative shoot apex of ponderosa pine on September 18, 1957* ($\times$ *70*).

November 29, 1957. A comparison between Figures 2 and 3 reveals graphically that a cone primordium made considerable growth between the first two collection dates. Increase in size had been accomplished primarily through meristematic activity of the cone apical meristem and its immediate derivatives. The cone was approximately 950 μ in width (at the base) and 1025 μ in height. The primary foliar appendages (bracts) of the cone were initiated first at the base of the cone and then acropetally thereafter in a definite phyllotactic pattern (Fig. 3). The uppermost portion of the cone was without appendages and was markedly rounded in outline.

A longi-sectional view of a cone of the same age revealed the following internal organization: a peripheral mantle of smaller cells densely cytoplasmic and showing considerable affinity for stains, and a large pith composed of larger cells many containing tannin (cells of dark appearance) (Fig. 6).

The cone apex exhibited essentially the same organization as that of a vegetative apex but it is not apparent at this magnification. The outer mantle was derived from the peripheral zone; the developing pith originated from the activity of the rib meristem (see discussion above and Fig. 1). Bract primordia were initiated from surface cells of the mantle.

February 18, 1958. Some growth occurred in the ovulate cones between November 29, 1957 and the February collection date; a cone increased slightly in width and height and several more bracts were initiated, but in general a cone had the same appearance as that of the previous collection. In all specimens the apical region remained dome-shaped.



FIGURES 2-4. *Entire, young ovulate cones of ponderosa pine dissected from terminal buds on September 18, 1957, November 29, 1957, and March 31, 1958, respectively.* FIGURES 5-7. *Median longitudinal sections of ovulate cones comparable in age to the entire cones which stand directly above them. See text for details.* FIGURES 2-4 *(× 18)*; FIGURE 5 *(× 70)*; FIGURES 6-7 *(× 25)*.

March 31, 1958. By this date a cone exhibited several morphological features not evident in the earlier collections. In addition to having greater width and height, the entire strobilus was conical in shape; the upper "free" portion of the apex was greatly restricted in area due to the continual acropetal formation of bracts (Fig. 4). The bracts were more than mere protuberances on the flanks of the cone axis. The marked contrast between the peripheral mantle of small, densely cytoplasmic cells and the larger, more vacuolate young pith cells is particularly well displayed in Figure 7. It will be noted that the bract primordia increased in size since the November and February collection dates and that in some instances the primordia are directed upward. Procambium —the precursor of vascular tissue—can be identified in some of the lower bract primordia.

May 1, 1958. The presence of young cones was easily detected by external examination of terminal buds on this date due to the relatively large size of the strobili. During the month of April a cone increased in width and height, the bracts attained approximately their final size, and the ovuliferous scales or "seed scales" were initiated in the axils of bracts. The ovuliferous scales were not visible externally; only the imbricated bracts with their rounded apices were apparent. The apex of the strobilus was always evident above the uppermost bracts at this stage of development (Fig. 8).

Ovuliferous scale primordia were quite evident in a cone when it was sectioned longitudinally. The axillary position of the scales is seen especially well in the upper portion of Figure 9, particularly on the left side. The "seed scales" eventually become dorsiventral, flattened structures with a pair of ovules on their upper or adaxial surfaces. No additional collections were made prior to the time of pollination.

FIGURE 8. *Portion of entire ovulate cone of ponderosa pine collected on May 1, 1958. Note the apical region which is "free" of appendages* (× *20*). FIGURE 9. *Median longitudinal section of cone comparable to that in Figure 8. Ovuliferous scale primordia are in evidence in the axils of bracts* (× *25*).

Discussion

As mentioned earlier, there have been several reports concerned with the time of cone initiation in *Pinus* for both microsporangiate and megasporangiate strobili. It is doubtful that a precise date for initiation can be established for any given species. Sampling over a period of several years would probably reveal yearly variations. Possibly this event could be anticipated within a two-week period, allowing for local yearly climatic variations. For *P. ponderosa*, in the vicinity of Placerville, California, ovulate cones could be detected microscopically by the middle of September 1957, but doubtless their actual initiation occurred one or two weeks earlier. Such information could not be applied directly to trees growing at higher elevations or in specialized environmental niches within the range of the species. Mergen and Koerting (1957) have called attention to this fact in relation to cone development for slash pine (*P. elliottii* Engelm.).

Because the vegetative bud in *P. ponderosa* enters an apparent dormant state one might conclude that the ovulate cone would cease growth with the advent of winter. The results of this study have shown that the cone continues to grow through the winter and early spring months in the vicinity of Placerville, California. An examination of the weather data recorded at the genetics station, Placerville, covering the time of the study indicated that the outdoor temperature frequently was high enough for limited periods for growth to occur. The cumulative effect would result in slow growth of the ovulate strobilus.

Continued growth of the ovulate strobilus has been reported by Mergen and Koerting (1957) for *Pinus elliottii* in Florida. These authors point out that it is quite possible for species of pines in the more southern latitudes to have a sustained growth period for both microsporangiate and megasporangiate strobili. Microsporangiate strobili of *P. elliottii* and of *P. ponderosa* enter a state of dormancy in the winter and the final ontogenetic stages take place the following spring. Since it would be of interest to determine the time of cone initiation in high alpine species of *Pinus*, a study has been undertaken to follow in detail the development of microsporangiate and megasporangiate strobili in *P. albicaulis* Engelm. and *P. contorta* Dougl. growing in the vicinity of Mt. Rose, altitude 8,500 feet, Sierra Nevada Range, California.

The time of initiation of strobili, particularly of the megasporangiate strobilus is of utmost importance in experiments concerned with increasing the production of strobili. If chemicals, for example, are to be utilized in an attempt to bring a young tree into earlier "flowering" or to increase cone production in older trees the date of initiation must be known if the applied agents are to be effective. Plans for pruning trees to convert more branches into strobili-bearing shoots should be based on a knowledge of cone initiation for a particular species. This information also is essential to investigations concerned with physiology of growth of the vegetative shoot and the strobilus.

Summary

Initiation of ovulate strobili in *Pinus ponderosa* growing in the vicinity of Placerville, California occurred during the first two weeks of September 1957. On September 18, 1957, the strobilus was approximately 300 μ wide and 125 μ high, and was devoid of appendages. Cytohistological zonation of the cone apex was essentially the same as that of the vegetative shoot apex. This correlation remained the same throughout all stages of cone development. While the vegetative shoots entered a rest period, strobili continued to grow throughout the late fall and winter. By November 29, 1957 a cone was 950 μ wide and 1025 μ high. Bract initiation had occurred acropetally but a considerable portion of the dome-shaped apex remained free of appendages. A strobilus continued to grow slowly and by May 1, 1958 it was conical in shape. Ovuliferous scale primordia were present in the axils of well developed bracts. The

observation that sustained growth occurs through the winter is in agreement with results reported by other authors for *Pinus elliottii*. Information on dates of initiation for microsporangiate and megasporangiate strobili for several species of *Pinus* is tabulated. The importance of knowing the date of cone initiation and tempo of development is discussed in reference to physiologic and genetic studies.

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New Editor of Forest Science

Effective January 1, 1960, Dr. John W. Duffie'd, Industrial Forestry Association, Nisqually, Washington, becomes the new Editor of FOREST SCIENCE, replacing Prof. Stephen H. Spurr who has held the position for the past five years. Correspondence concerning manuscripts submitted for publication should now be addressed to Dr. Duffield.

Wood Technology Handbook

Holztechnologisches Handbuch, Band II. [*Wood Technology Handbook, Vol. II*] *by L. Vorreiter. xii, 646 p., 354 illustrations, 68 tables. G. Fromme, Wien/Muenchen, 1958 (in German). $15.50.*

Review by Arno P. Schniewind
University of California Forest Products Laboratory
Richmond, California.

This volume of the wood technology handbook is the second of a proposed series of three. The volume is divided into sections on: (1) wood-moisture-heat relations, (2) wood drying, (3) heating wood in steam and water, and (4) various processes of giving wood shape without the removal of chips.

The section on wood in relation to heat and moisture deals with the various constants and parameters that determine these relations and with the exchange of heat and moisture. Information on the measurement and control of temperature and relative humidity is also included. This section is particularly well organized and contains the fundamental concepts which form the basis for the next section on wood drying. The subject of wood drying takes up approximately half of the entire volume. The discussion begins with air-drying, and continues with "artificial air-drying" methods which might best be classified under the heading of pre-drying. This is followed by thorough treatment of conventional kiln drying and a valuable discussion of high temperature drying. Information on various special methods is given, including vapor drying, solvent seasoning, chemical seasoning, vacuum drying, as well as drying with radiant and electrical energy, the latter both at low and high frequency.

The section on heating wood in steam and water is concerned with various practical aspects of these processes and the last section deals with such "chipless" forming processes as compreg manufacture, steam bending, and the manufacture of molded plywood.

Whenever possible the subject matter has been put on a mathematical basis. Although in many cases this is very empirical, and in some cases, such as the calculation of drying time, too cumbersome as yet to be practical, such an approach is highly desirable and ultimately will be the most useful one. Liberal use has been made throughout of sample calculations to illustrate the use of various mathematical expressions.

The author has drawn on the world literature in the field to provide a wealth of information. The contents are well proportioned in emphasis within the scope of the volume, and their logical arrangement should facilitate its use as a valuable reference book. In this respect the subject matter index appears to be satisfactory.

Because of a certain continuity and interdependence of subject matter in the text and the many symbols introduced throughout the volume the prospective reader armed with a dictionary but little knowledge of the German language will have considerable difficulty in extracting wanted information. For anybody with a fair knowledge of scientific German the book should be a welcome addition to the literature in the field of wood technology. It is to be recommended particularly to wood technologists who are interested in an engineering approach to dealing with wood.

Pollen Germination of Pinus As Affected by the Environment

BY
J. R. McWILLIAM

PINE POLLEN germinates soon after it arrives on the receptive surface of the nucellus. Before reaching the nucellus, the pollen is immersed in the micropylar fluid (McWilliam, 1958). It is not known how long the pollen remains in this fluid, but it is probably only for a few hours. From observation of ovules which were dissected at varying intervals after pollination, it was found that the fluid is no longer present at the time of pollen germination. Thus, any influence that this fluid might have on the pollen would have to take effect during this period of immersion, while the pollen is transported to the nucellus. It seems unlikely, under these conditions, that the micropylar fluid acts as an incompatibility sieve against foreign pollen. After germinating, the pollen tube grows towards the apex of the nucellus, irrespective of the location and orientation of the pollen grain. This suggests some form of tropic influence at this stage (Fig. 1). Germination and pollen tube growth take place in darkness, and probably under conditions of low oxygen concentration, because the micropylar canal closes soon after pollination (Fig. 2). After the pollen tube has entered the nucellus, it grows slowly and usually in an irregular and branched fashion, and after a period of 12 months it has penetrated only a short distance from the apex of the nucellus. Just prior to the maturation of the egg cell, which is approximately 13 months after pollination, the pollen tube grows rapidly through the remainder of the expanded nucellus and discharges its contents into an archegonium (Fig. 3). The endogenous carbohydrate reserves of the pollen are not sufficient to support growth over this period, and the pollen tube must therefore obtain supplementary food from the surrounding nucellar tissue. For this reason, the ability of the germinating pollen to absorb such food, and in particular carbohydrates, from the cells of the nucellus during this period, must be an important factor in its survival and growth.

During this lengthy period of pollen tube growth, many factors of the environment, both chemical and physical, are operating to determine its successful outcome. An attempt has been made in this study to isolate some of these factors, and determine their effect on pollen germination and growth *in vitro*. Such information should be helpful in understanding the limitations imposed on successful pollen germination in nature, particularly following pollination between two different species. For this purpose the following studies were undertaken: (1) behavior of pollen when ger-

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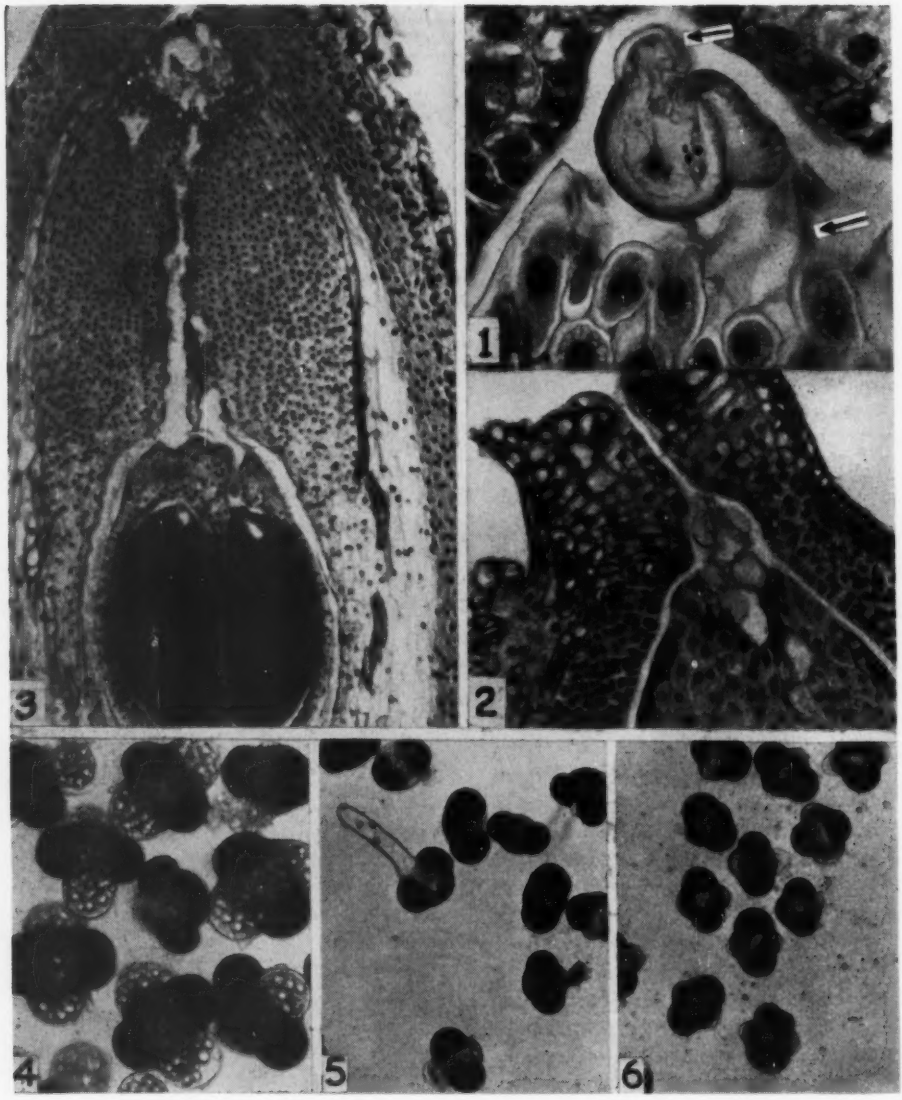
The author is a Research Officer with the Division of Plant Industry, C.S.I.R.O., Canberra, Australia. This publication is based on part of a dissertation submitted to the Graduate School of Yale University in partial fulfilment of the requirements for the Ph.D. degree. Manuscript received Jan. 30, 1959.



FIGURES 1-6. *Development of Austrian pine pollen within the ovule, and under conditions* in vitro. FIGURE 1. *Germination of an inverted pollen grain, with the pollen tube (arrows) curving around to penetrate the nucellus (× 310).* FIGURE 2. *Ovule one month after pollination, showing the development of the pollen tube, and the closing of the micropyle (× 120).* FIGURE 3. *Ovule at the time of fertilization, showing the path of the pollen tube through the nucellus. The region at the apex of the nucellus bordered by the zone of dead cells represents the extent of pollen tube penetration during the first 12 months following pollination (× 45).* FIGURE 4. *Pollen cultured in micropylar fluid. The abortive pollen tubes are short and swollen and have accumulated starch (× 170).* FIGURE 5. *Poor germination of pollen at pH 4 (× 100).* FIGURE 6. *Inhibition of pollen germination at pH 8 (× 100).*

minated in micropylar fluid, (2) influence of hydrogen-ion concentration on pollen development, (3) role of sucrose as an exogenous substrate for pollen germination, (4) tropisms and pollen tube growth, (5) effect of light and oxygen on pollen germination and tube growth, (6) the "clumping factor" in pollen germination, (7) behavior of pollen when germinated in the presence of pollen of another species.

Review of Literature

The occurrence of promoting or inhibiting substances in the stigmatic secretions of flowering plants has been suggested by Yasuda and Arai (1927), O'Connor (1928), Addicott (1943), and Pyatnitski (1947).

The ovules of *Pinus nigra* Arn. secrete a small drop of fluid from the micropyle at the time of pollination (McWilliam, 1958). Echols and Mergen (1956) found that aqueous extracts of micropylar fluid from strobili of *Pinus elliottii* Engelm. reduced the germination of pollen *in vitro*, and that this effect became more pronounced with increasing concentrations of the extract. Kühlwein (1937) showed that the germination of *Taxus* pollen in micropylar fluid extract was superior to the results obtained in sucrose.

The optimum pH range for the germination of pollen of several conifer species has been determined by Kühlwein (1937). For pine, he obtained best germination between pH 4.5 and pH 6.0. Johnson (1943) successfully germinated pine pollen on agar at pH 7.3, but was unable to germinate it under similar conditions at pH 4.8. Smith (1939) and Takeuchi (1953) used a basic water-agar medium at pH 6.4 and pH 6.7, respectively, for germination studies with pine pollen. It is not clear why these values were chosen, but in both cases good germination was obtained. Brink (1925), and Sato and Muto (1955) have found that the optimum pH range for the pollen of a number of flowering plants is between pH 5.0 and pH 8.0.

Sugars, and sucrose in particular, have been used extensively in aqueous solutions to study the germination of gymnosperm pollen. Green (1894) used sucrose for the germination of *Zamia* pollen. Dengler and Scamoni (1939) germinated several species of pine pollen in a range of sucrose solutions from 5 to 40 percent, and obtained the best germination at the lowest concentration. Five to ten percent sucrose has been used commonly to supplement the basic medium for germinating pollen of *Pinus* (Smith, 1939; Duffield and Snow, 1941; Johnson, 1943; Takeuchi, 1953; Echols and Mergen, 1956; Dillon and Zobel, 1957). Kühlwein (1937) and Tanaka (1955) have reported that approximately 0.1 percent sucrose gives maximum germination and tube growth.

The accumulation of starch in the developing pollen tubes of pine has been reported by Tischler (1917), Kühlwein (1937), Marcet (1951), Takeuchi (1953), Tanaka (1955), Dillon and Zobel (1956), and Hellmers and Machlis (1956). In a detailed study of the sugars utilized by *Pinus ponderosa* Laws. pollen during germination, Hellmers and Machlis (1956) established the ability of the pollen to absorb and metabolize a variety of mono-, di-, and trisaccharides. They showed further, that when germinating pollen was supplied with sucrose it continued to develop actively for a long period after pollen which was entirely dependent on endogenous reserves had begun to die. This also had been demonstrated by Tanaka (1955) with pollen of *Pinus densiflora*. Tulecke (1957) used sucrose to promote the germination of *Ginkgo* pollen, but he found that this medium, unlike more complex nutrient media, did not permit the gametophyte to mature.

A search of the literature did not reveal any studies of tropistic responses of pollen tubes in conifers. However, Brink (1924) and Tsung-Hsun (1949) have studied

pollen tube chemotropism in a large number of angiosperms. They were able to demonstrate it in only a comparatively few species. Wulff (1935) and Ziejlemaker (1956), on the basis of their results, suggested that the orientation of the pollen tube in its growth from the stigma to the ovary in flowering plants is controlled by electrical forces.

The effect of light on the germination of pine pollen has been investigated by Johnson (1943), who found that it had no effect on germination, but that it caused an increase in pollen tube length. Werfft (1951) claimed that sunlight had an adverse effect on pollen viability, and attributed it to the effect of ultra-violet light. Adams (1916) found that germination of apple pollen was unaffected by light, but that it failed in the absence of oxygen. In *Pinus*, according to Hellmers and Machlis (1956), the pollen tube *in situ* becomes morphologically isolated from oxygen as a result of the closing of the micropylar canal. In support of this, they were able to demonstrate anaerobic utilization of endogenous sucrose by the pollen of *Pinus ponderosa* during the first 24 hours after wetting. However, the rate of utilization was only half of that in air.

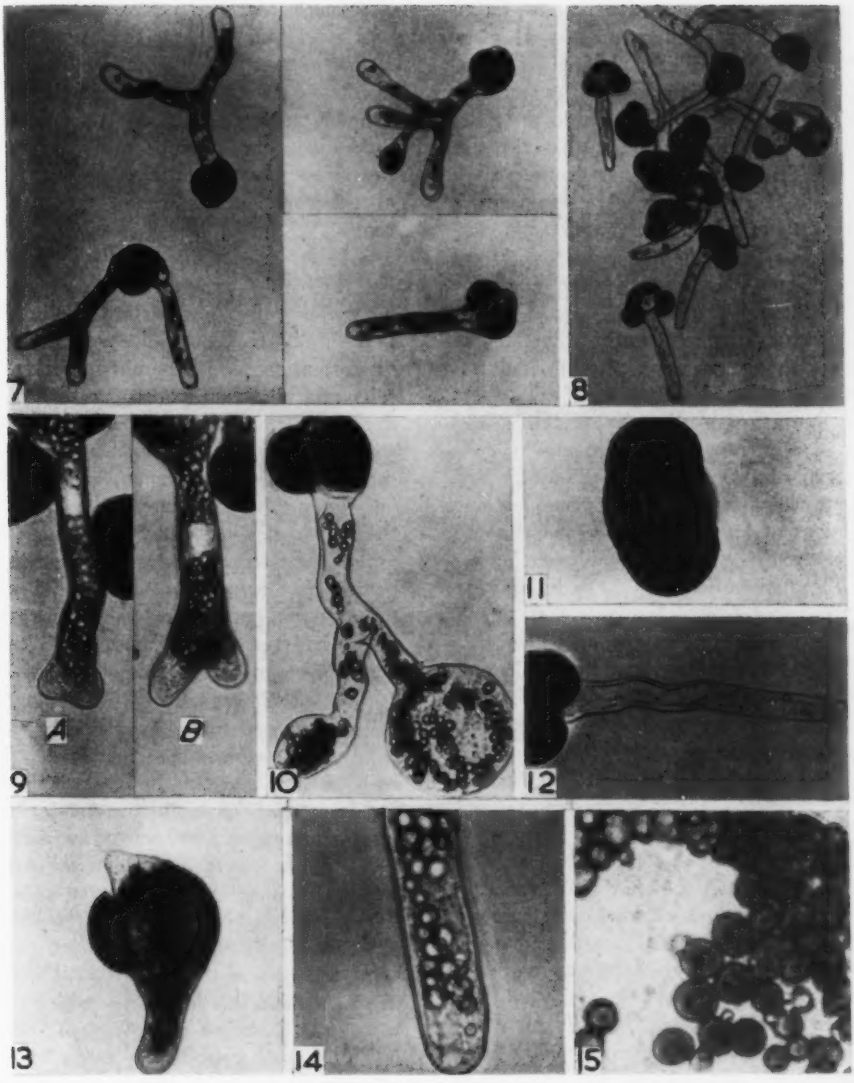
The beneficial effect of "clumping" or aggregating on the germination of pine pollen has been observed by Duffield (1954). A similar response has been recorded with pollen from a number of flowering plants (Brink, 1924; Kühlwein, 1937; Kuhn, 1937; Smith, 1942; Addicott, 1943), and all authors suggested that some growth promoting substance was involved. Working with a wide range of flowering plants, Loo and Hwang (1944) found that indoleacetic acid (IAA) stimulated pollen germination, when used in low concentration (10^{-10}M) Kato (1955) and Chandler (1957) obtained a similar effect with gibberellic acid. With *Pinus*, the results have been quite variable. Huang (1948) obtained no response to auxins and other indole compounds, whereas Smith (1939, 1942) found that IAA stimulated pollen germination. Echols and Mergen (1956) obtained slight stimulation with indolebutyric acid, but inhibition with IAA.

Material and Methods

The pollen used in this study was collected from mature trees of three species: Austrian pine (*Pinus nigra* Arnold), red pine (*P. resinosa* Ait.), and ponderosa pine (*P. ponderosa* Laws.). The collections were made from a minimum of three trees of each species, and the pollen was stored at 4°C and 25 percent relative humidity. Two methods of germination were used. Both were modifications of the hanging drop technique as described by White (1954, p. 100). In the first, the pollen was germinated in a drop suspended from a cover slip, and in the second, the drop was replaced by a 1 cm^2 wafer of 0.75 percent Bacto agar (Takeuchi, 1953). A Van Tieghem cell was cemented to the glass slide to provide the moisture chamber. Double-distilled water, pH 5.6, (distilled in Pyrex) was used as the basic medium in both methods, and it was used throughout as the medium for the controls. The cultures were incubated in the dark for 120 hours at 26°C to ensure maximum germination.

Percentage germination was based on the average of 150 pollen grains counted at random in each replication, with a minimum of four replications for each experiment. Pollen was considered to have germinated if the length of the pollen tube was equal to, or greater than the small diameter of the pollen grain. The average pollen tube length was based on ocular micrometer measurements ($\times$ 125) of ten unbranched pollen tubes selected at random in each replication. Austrian pine pollen was used as the general experimental material throughout, and this species is implied when referring to pollen, unless otherwise stated.

Micropylar fluid was extracted from re-



FIGURES 7–15. *Effect of sucrose on the development of pollen tubes of Austrian pine.* FIGURE 7. *Four basic types of pollen tube development found in sucrose solutions. The proportion of each type depends on the concentration of sucrose (× 140).* FIGURE 8. *Pollen germinating in distilled water showing the preponderance of unbranched pollen tubes (× 120).* FIGURE 9. *Development of a forked pollen tube. A. Retarded growth at the apex. B. Formation of two side branches (× 340).* FIGURE 10. *Swollen pollen tube, found in culture containing sucrose (× 280).* FIGURE 11. *Pollen grain imbibed for 12 hours in distilled water showing small starch grains (× 360).* FIGURE 12. *Same as Figure 11 after 9.6 hours (× 280).* FIGURE 13. *Accumulation of starch grains in a pollen tube after 48 hours incubation in sucrose solution (× 320).* FIGURE 14. *Starch grains accumulating in a pollen tube a short distance from the apex (× 560).* FIGURE 15. *Detail of starch grains, showing the characteristic shape and lamella (× 820).*

ceptive strobili of Austrian pine by means of a fine glass capillary tube as described previously (McWilliam, 1958). The extract was used immediately to establish hanging drop cultures similar to those described, with the exception that the size of the drop was reduced to conserve the extract. Thirty cultures were set up in this way, half of which were sown with Austrian pine, and the other half with red pine pollen. Four controls were set up for each species.

To study the response of pollen to the pH of the germination medium, cultures were established using distilled water which was adjusted with $KHCO_3$ and HCl, to a range of hydrogen-ion concentrations from pH3.0 to 8.0. Standard citrate-phosphate and phosphate buffer solutions of known pH were found to be unsatisfactory even at high dilution, owing to the toxic effect of the salts on the pollen.

The influence of sucrose on pollen germination was investigated by culturing pollen at eight different concentrations of sucrose, from 0.0 to 0.3M. Observations were also made on starch formation and branching characteristics of the pollen tubes. The presence of starch was verified by the standard I_2KI test.

To obtain data on the rate, extent, and duration of pollen tube growth on a medium which was supplied with sucrose, pollen was germinated on sucrose-agar blocks (0.01M), and measurements made daily for a period of 14 days. Pollen germinated on water-agar was used for comparison purposes. The average pollen tube length was based on the measurement of 50 vigorous, unbranched pollen tubes (10 per replication) taken at random for each successive measurement.

The possibility of the existence of chemicals in the nucellus which cause a tropistic response of pollen tubes was investigated as follows. Nucellar caps were sectioned from 20 unpollinated, receptive Austrian pine ovules. These were mounted in water-agar blocks so that the apex of the nucellus was level with the surface of the agar. Pollen of Austrian pine and red pine was distributed evenly over the surface of the agar by tapping it from a glass rod. After incubation, the cultures were examined microscopically to determine the orientation of the pollen tubes around the nucellar caps.

The effect of light on pollen germination and tube growth was observed by incubating pollen under constant illumination (600 fc) supplied by "daylight" fluorescent tubes, and comparing these results with those of pollen germinated in darkness. The response to oxygen was studied by germinating pollen in an atmosphere devoid of oxygen, and comparing the results with those germinated in the presence of atmospheric oxygen. The oxygen-free atmosphere was obtained by germinating the pollen in a closed container in an atmosphere of dry nitrogen, which had been bubbled through alkaline pyrogallol to remove traces of oxygen.

The stimulatory effect of clumping on pollen germination was examined by comparing the germination of clumped pollen with that of scattered pollen when cultured on agar. The clumped pollen cultures represented a density of more than 1,000 pollen grains /cm,^{2} and the grains were often close enough to be in contact. The scattered (sparse) cultures represented a density of about 25 pollen grains /cm^2 and were never in contact. To stimulate germination in sparse pollen cultures, four additives were used to supplement the basic germination medium: (1) 0.01 M sucrose, (2) 0.2 to 1.0 mg /l of IAA, (3) dead pollen, (4) extracts from germinating pollen. The first two were incorporated in the germination medium, whereas the dead pollen [heat killed; 24 hours at 75°C (Hodgkins, 1952)] was scattered over the agar containing a predetermined number of fresh pollen grains. The pollen extracts were obtained by germinating pollen on the upper

surface of a thin, two-layer agar block. After 60 hours, the upper layer with the germinating pollen was removed, and the sparse cultures were established on the pollen-free surface of the lower block. Ten replications were used for each treatment.

The effect of mixing pollen of different species on subsequent germination was investigated in three species, Austrian pine, red pine, and ponderosa pine. Equal quantities of pollen were thoroughly mixed in distilled water before setting up the cultures, and the results were compared with the germination of the same pollen in pure culture.

Results

Micropylar fluid. Pollen of both Austrian pine and red pine failed to germinate in the Austrian pine micropylar fluid, whereas the controls of both species developed normally. This failure became quite apparent after 48 hours, as was evidenced by the ruptured pollen tubes and extruded contents. Most pollen grains of both species accumulated starch, and became swollen (Fig. 4). This starch was probably derived from the sugars present in the micropylar fluid. After 96 hours the condition of the pollen remained unchanged, but the contaminating bacteria and fungal hyphae had multiplied and spread throughout the medium. No contamination of this type was evident in the controls. The possibility of the inhibition being caused by the sugars present in the micropylar fluid was investigated by culturing Austrian pine pollen in a distilled water medium that contained the same concentration of the three sugars (sucrose, glucose, and fructose) known to be present in the extracts (McWilliam, 1958). This mixture gave no indication of inhibition, and germination was actually superior to that of the controls.

Influence of pH. The results of pollen germination and tube length over a wide range of pH values are summarized in Figure 16, where percent germination and

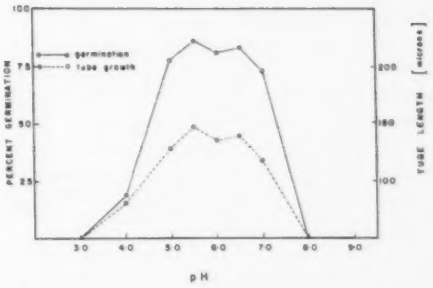


FIGURE 16. *Effect of hydrogen-ion concentration on germination and tube growth of Austrian pine pollen.*

tube length are plotted against the pH of the germination medium. There appeared to be no sharply defined pH optimum, and over the range of pH 5 to 7 there was no significant difference in either pollen germination or tube length. Pollen germination and tube development over this range appeared quite normal. At pH 4, although some germination occurred, the pollen tubes were short, and plasmoptysis was common (Fig. 5). No germination was recorded below this value, or at pH 8 (Fig. 6).

Role of sucrose. The response of pollen germination to varying concentrations of sucrose is summarized in Figure 17 where percent germination is plotted against log concentration of sucrose. An analysis of

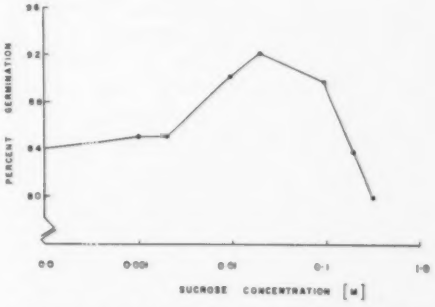


FIGURE 17. *Effect of sucrose concentration on germination and tube growth of Austrian pine pollen.*

these data indicated a highly significant response to concentration. The highest germination occurred over a range of concentrations from 0.10 to 0.01 M, with a maximum at 0.05 M. Tube growth, however, appeared to be more vigorous at even lower concentrations. Only one concentration (0.3M) resulted in germination which was inferior to the controls.

The addition of sucrose to the germination medium increased the number of double and branched pollen tubes, by comparison with the number present in the distilled water controls (Figs. 7, 8). Maximum branching occurred at approximately the same concentration as that which gave maximum germination. Practically all branching was initiated in the pollen tubes at a point corresponding to the position of the tube apex after incubation for 48 hours. At this stage the growth at the apex slowed down, and the first two side branches started to form (Fig. 9). The swelling of pollen tubes (Fig. 10) was observed only in cultures containing sucrose, and mostly at the higher concentrations.

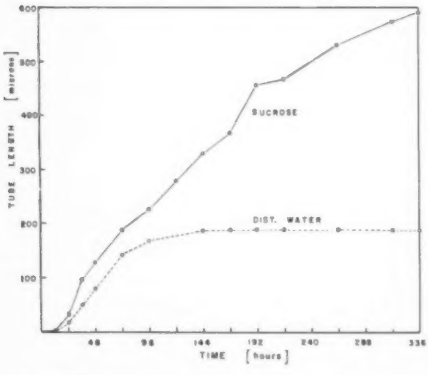


FIGURE 18. *Effect of sucrose on the rate, extent, and duration of pollen tube growth of Austrian pine. The pollen was germinated on sucrose-agar (0.01M). Each point on the graph represents the average length of 50 pollen tubes taken at random at each measurement. Pollen germinated on water-agar was used for comparison purposes.*

Starch formation was active at all the concentrations of sucrose used. Accumulation commenced before the pollen tube emerged, and continued during its development, providing the substrate had not been exhausted (Figs. 13, 14). As the growth of the pollen tube slowed down, the starch grains tended to accumulate a short distance back from the growing point. The characteristic shape and lamella of the starch grains at this time can be seen when lightly stained with I_2KI (Fig. 15). By way of contrast, when pollen is germinated in distilled water, the small starch grains initially present are soon utilized, presumably to support the growth of the developing pollen tube (Figs. 11, 12).

The effect of sucrose on the rate, extent, and duration of pollen tube growth is summarized in Figure 18, where tube length is plotted against time. Pollen germinated more rapidly when sucrose was present in the medium; however, the growth rate for the first 72 hours was practically the same in both sucrose and distilled water. After this time, the growth rate of the pollen tubes in distilled water declined sharply, and ceased after 168 hours when the average length was 188 μ. In the sucrose medium, growth continued at a slightly decreased rate, and the tubes reached an average length of 590 μ after 336 hours, at which time the measurements were discontinued. The decline in growth rate in both cases is accompanied by vacuolation of the cytoplasm, and the disappearance of starch grains from the pollen tube.

Chemotropism. No evidence of pollen tube chemotropism could be observed when nucellar tissue from receptive ovules was used. Pollen of both Austrian, and red pine germinated readily in the presence of, and often in contact with this tissue, and there was no indication of any preferred orientation of the pollen tubes.

Light and oxygen. Germinating pollen in the presence of light, and under anaerobic conditions, made no difference to its sub-

sequent behavior. When compared with the controls, there was no significant difference in the means for either pollen germination or tube growth under these conditions.

Clumping. The effect of pollen density on the germination of pollen *in vitro* is summarized in Table 1. Under these conditions scattered pollen showed practically no germination, whereas clumped pollen cultures showed normal, vigorous development. A highly significant increase in germination was obtained in sparse pollen cultures by the addition of dead pollen, or extracts from living pollen. This same response could not be induced by the addition of sucrose or IAA in the concentrations used.

Mixing pollen from different pine species had no effect on its subsequent germination. It is not posible to recognize individual species of pine when the pollen is mixed, unless there is a marked difference in the size of the pollen grains.

TABLE 1. Pollen germination at different densities and the effect of added nutrients.

Density	Germination medium	Average germination Percent
Clumped	Agar	90
Sparse	"	1
Sparse	Agar + sucrose	1
Sparse	" + IAA	3
Sparse	" + dead pollen	43
Sparse	" + extract of germ. pollen	41

Discussion

The fact that pollen fails to germinate in the micropylar fluid supports the view that this secretion is a temporary phenomenon, and that the fluid is no longer present in the ovule when the pollen germinates on the nucellus. Pollen undoubtedly becomes imbibed in this fluid, and in this way possibly receives the initial stimulus for germination. It seems unlikely that the micropylar fluid acts as an incompatibility sieve which discriminates against foreign pollen, because both species, Austrian pine and red pine, failed to germinate when cultured in pure extracts.

The presence of sugars in the micropylar fluid was verified by the accumulation of starch in the pollen of both species when they were cultured in this fluid. O'Kelley (1957) found that pollen germination of *Tecoma* could be inhibited by supplying sucrose along with a number of other sugars, including fructose. Such an explanation for the inhibition observed in this study seems unlikely, in view of the vigorous pollen germination obtained in an artificial mixture of sugars, similar in composition and concentration to those in the natural fluid. Some other factors, or substances, associated with the fluid must be responsible. Working with a variety of plants, Curtis (1943, a, b) and Wilson (1923) have found inorganic salts in extracts of guttated fluids that were toxic to the foliage. A similar factor may be responsible for the inhibition experienced in the micropylar fluid, because pine pollen is sensitive to the presence of metallic ions. This was shown in preliminary studies by its failure to germinate in tap water. The development of fungal mycelia and other micro-organisms was vigorous in all cultures involving the micropylar fluid. There was no evidence to suggest that the growth of such organisms is inhibited by substances present in the fluid.

The possibility of the hydrogen-ion concentration becoming a limiting factor *in vivo* seems unlikely, in view of the wide range of tolerance to pH exhibited by pollen germinated *in vitro*. Also, the average pH of cell sap and plant exudates falls well within the limits of this range (Wilson, 1923; Hurd-Karrer, 1939). Unfortunately, it was not possible to obtain sufficient micropylar fluid to determine its pH accurately.

The optimum concentration of sucrose for the germination of Austrian pine pollen appears to be considerably lower (0.1 to

0.01M) than that which has been used in previous studies with pine pollen. The bifurcation, swelling, and the formation of double tubes was increased from five to eight fold when pollen was cultured in a sucrose medium. This type of development appears to be characteristic of the behavior of pollen tubes growing in the apex of the nucellus (Fig. 3). In *Ginkgo*, Tulecke (1957) found that haustorial development in pollen tubes was dependent on the concentration of sucrose in the external medium. The nature of the stimulus causing such growth behavior is not clear. Tanaka (1955) suggested that sugar in the external medium may stimulate increased respiration, resulting in accelerated uptake of water. When this uptake is not accompanied by comparable growth of the pollen tube wall, it results in the deformation and swelling of the growing tip, leading to bifurcation. Iwanami (1956) determined that branching could be induced in pollen tubes of *Lilium* by the addition of 2,4-D to the germination medium. Whatever factor is responsible, it probably acts in some way to interfere with the synthesis of the pollen tube at its apex, where growth is taking place. Branching commences approximately 48 hours after starting the cultures, and coincides with the build-up of the fungal and bacterial population in the medium. It is possible that enzymes, or other by-products of such micro-organisms, could be responsible for the disruption of the growing point.

The ability of pollen to absorb and utilize externally supplied carbohylrate may explain how it is able to survive for 13 months in the nucellar tissue prior to fertilization. The presence of starch grains in the cytoplasm of pollen tubes of *Pinus* just prior to fertilization would tend to support this view (Coulter, 1897). The fact that sucrose in the germination medium increases the growth and prolongs the life of pollen was clearly demonstrated. Measurements of sections of Austrian pine ovules two weeks after pollination, revealed that the average distance from the apex of the nucellus to the developing gametophyte was 400 μ. On the basis of the growth of the pollen *in vitro*, the tubes would be capable of reaching the ♀ gametophyte within about 7 days. However, in nature, the pollen tubes penetrate, on the average, for a distance of only 320 μ during the first 12 months. At this time, due to the growth of the nucellus, 1200 μ separate the apex of the nucellus from the neck cells of the archegonia (Fig. 3). The fact that the pollen tubes can grow further in seven days on a dilute sucrose medium than is normally achieved *in vivo* in 12 months, indicates that some restraining influence is operating in the nucellus to delay tube growth. This would appear to be in the form of an inhibition, or the lack of a specific enzyme or stimulus, because about 9 to 10 days before fertilization, the pollen tube grows directly through the remaining 900 μ of the nucellus to release the male nuclei into the fully mature egg cel (Fig. 3).

The initial orientation of the pollen tube growth towards the apex of the nucellus, does not appear to be the result of a chemical stimulus, although conditions may differ somewhat *in vivo*. Also, it is apparent that Austrian pine nucellar tissue contains no water-soluble substances that are detrimental to the germination of red pine pollen. The possibility of a negative geotropic force being involved is suggested by the marked vertical orientation of the ovules during, and for a short time, after pollination. The evidence from inversion experiments, however, does not support this view, as pollen of Austrian pine germinated vigorously in ovules whose normal vertical orientation had been reversed. (McWilliam, 1958).

With respect to light and lack of oxygen, neither factor appears to be limiting for pollen germination. In the case of oxygen, although every effort was made to exclude it from the atmosphere surrounding the germinating pollen, it is not known if all traces were completely removed. However, it is clear that pollen is capable of germinat-

ing, and making active tube growth under conditions of extremely low oxygen tension. This supports the view of Hellmers and Machlis (1956), that pine pollen is a facultative anaerobe, and explains its ability to function efficiently in the enclosed tissue of the strobilus.

The inability of a lone pollen grain to germinate *in vitro* indicates that some additional factor, or higher concentration of a factor already present, is necessary to initiate germination. These conditions are satisfied when the number of pollen grains per culture is increased, or when aqueous extracts of dead or germinating pollen are supplied to the medium. The factor is water soluble, and is not a product of the metabolism of germinating pollen. Also, it is non-specific, as pollen from different species germinated freely in mixtures, and showed no evidence of inhibition. This factor is apparently present in the ovule, as single pollen grains are frequently found germinating on the nucellus, and the maximum number found was rarely in excess of three or four.

Summary

Austrian pine pollen was germinated under a variety of conditions similar to those experienced *in vivo*. Limited tests of a similar nature were also carried out with pollen of red pine and ponderosa pine. The effect of these factors was studied individually, and their limitations on the germination of pollen *in vivo* was determined. Pollen of Austrian and red pine failed to germinate in Austrian pine micropylar fluid, indicating that this fluid is a temporary phenomenon, and not the medium for pollen germination in the ovule. Pollen germination was recorded over a range of hydrogen-ion concentrations from pH 4.0 to 7.0. Germination was unaffected by the presence of light, or by a severe deficiency of oxygen in the external medium. The optimum concentration of sucrose for maximum germination was between 0.10 M and 0.01 M. It caused an increase in bifurcation, and the formation of starch grains in the pollen tubes. The extent and duration of pollen tube growth was increased threefold by the presence of sucrose in the medium. Under these conditions, the pollen tubes grew further in seven days than they normally grow in the ovule during the first 12 months following pollination, indicating the existence, *in vivo*, of some form of restraining influence. The beneficial effect of clumping on pollen germination was demonstrated, and percentage germination of scattered (sparse) pollen cultures was increased by the addition of extracts from dead and germinating pollen. The non-specific nature of this stimulus was demonstrated by the successful germination of mixtures of pollen from two different species.

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A Summary of Pine Genetics Studies

Züchtung mit Kiefern. Teil I. Individualunterschiede und Provenienzversuche. Teil II. Kreuzungen, Resistenzzüchtung und Zytologie. (Breeding with pines. Part I. Individual differences and provenance tests. Part II. Crossing, resistance breeding, and cytology.) By P. Schütt. Mitteilungen der Bundesforschungsanstalt für Forst-und Holzwirtschaft, Reinbek bei Hamburg Nos. 40 and 42. 1958 and 1959. 65 and 40 pp. Lithoprinted. Buchhandlung Max Wiedebusch, Hamburg. Available from author, Institut für Forstgenetik und Forstpflanzenzüuchtung, (24a) Schmalenbeck über Ahrensburg, Siekerlandstrasse 2, Germany.

Review by Jonathan W. Wright
Michigan State University, East Lansing

Dr. Schütt, one of several top-flight tree breeders on the staff of the Institut für Forstgenetik und Forstpflanzenzüchtung at Schmalenbeck, West Germany, is well qualified to undertake the type of summarizing job which this German paper represents. He accomplished what is rarely seen in such writing: the inclusion of as many pertinent references from America, the southern hemisphere, and Japan as well as from Europe. What is more, he seemed to be familiar enough with these non-German references that he was able to give the proper weight to each. That and a good, clear organization pattern make the papers very usable, even for readers who are not fluent in German. They probably constitute the most complete and most useful world-wide summary of work on the genetics of the pines that has yet appeared.

The books consist of six sections. There is a short introduction which includes background information and general references on pollination technique, vegetative propagation, flowering biology, and other borderline areas of genetics. Next follows a short but complete section describing the results obtained in clonal and progeny tests. The third and fourth sections, on provenance testing and species hybridization, are the longest. Here Schütt has done an especially good job of including maps, short tables, and diagrams to illustrate the most important conclusions regarding each species or cross. Then at the last are short sections on resistance breeding and cytology. Detailed tables of contents and author indexes, plus a rigorous adherence to his outline make the whole work easy to use as a reference.

Stalactiform Rust on Jack Pine in Minnesota

BY
NEIL A. ANDERSON

DURING THE SUMMER of 1957 elongated diamond-shaped cankers were observed on mature jack pine (*Pinus banksiana* Lamb.) in north central Minnesota. The cankers were similar to those described by Mielke (1956) and Meinecke (1920) caused by stalactiform rust [*Peridermium stalactiforme* Arth. & Kellem., *Cronartium coleosporioides* Arth. (Arthur, 1934)] on lodgepole pine (*Pinus contorta* Dougl.) in the West. In May, June, and July of the following year hundreds of these cankers were found on mature jack pines, but aeciospores were found on only three trees. In September pycnial exudate and pycniospores were found on the margins of many of the cankers, but by October almost all of the tissue on which pycnia previously were present had been eaten by rodents.

In one of the areas many young jack pine trees about 3 feet high were severely cankered by what appeared to be the same rust. On a 1/10-acre plot aeciospores were collected from 30 cankered trees. These aeciospores did not resemble those of *Cronartium comandrae* Peck, and the alternate hosts of *C. comptoniae* Arth. were not encountered in the area.

Plants of Indian paintbrush (*Castilleja coccinea* L.), cow-wheat (*Melampyrum lineare* Desr.), lousewort (*Pedicularis canadensis* L.), and sweetfern (*Comptonia peregrina* (L.) Coulter) were dug up in the field, planted in pots, and transferred to the greenhouse in St. Paul. Various genera of the Scrophulariaceae are reported to be alternate hosts of *Cronartium coleosporioides* (Arthur, 1922), and sweetfern is an alternate host of *C. comptoniae*. Plants were left for 3 weeks to allow any natural infection to develop, and no rust infection became evident on them. Two or three plants of each species were then inoculated separately with spores from each of two cankers on mature trees, incubated for 24 hours at 100-percent relative humidity, then kept in a chamber at 75° F. Uredia and telia, characteristic of *Cronartium coleosporioides*, developed on *Castilleja coccinea* and *M. lineare*, but not on *P. canadensis* or *Comptonia peregrina*. Noninoculated plants of all four species remained free of rust.

Castilleja coccinea was grown from seed in the greenhouse during the winter of 1958-59. This precluded any possibility of natural infection. Six to ten plants were grown in each of several pots. Eight collections of aeciospores were used in inoculating the *Castilleja*. Three collections were from cankers on mature trees and five were from cankers on small trees. Only one collection of spores was used to inoculate the plants in a single pot. The inoculations

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When this paper was written, the author was a forest pathologist at the Lake States Forest Experiment Station, Forest Service, U. S. Department of Agriculture. He is now in the Department of Plant Pathology and Botany of the University of Minnesota.

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were replicated several times at intervals of a few weeks. Uredia and telia formed on all the 128 inoculated plants; 40 non-inoculated controls maintained under the same conditions remained free of rust infection.

So far as the writer is aware, *Peridermium stalactiforme* (*Cronartium coleosporioides*) has not been reported previously on jack pine in Minnesota or any other state east of the Rocky Mountains, although it has been reported on jack pine in Canada (Riley *et al.*, 1952). Also, symptoms ascribed to *P. harknessii* Moore or *P. filamentosum* Peck.[1] (Mielke, 1952) have not been observed on jack pine in the north central area of the state where the rust here described was found.

[1]For clarification of the nomenclature of the species of *Peridermium* referred to, see comments by Cummins and Stevenson (1956) under *Cronartium coleosporioides* Arth.

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Systematic Sampling With Multiple Random Starts

BY
CHERNG-JIANN SHIUE

IN FOREST SURVEYS, it is a general practice to select a sample consisting of a small fraction from a forest on which we wish information. Based on the facts learned by examining the sample, inferences about the forest are made. It is the sample, a small fraction of the forest, that we observe, but it is the population, the whole forest, that we seek to know.

The true value of a characteristic of a population is called a "parameter." The estimated value of the characteristic based on the observations from the sample is called a "statistic." The statistic is an estimator of the corresponding parameter. For instance, the true timber volume of a forest is a parameter which exists in nature but would be very costly to measure. By investigating a certain number of sample plots properly selected from the forest, a "blown up" estimate of the timber volume for the whole forest can be made. Such an estimate is a statistic. Any statistics, or estimates of parameters, are naturally subject to the errors of sampling, and it is important to make some statement about the probable size of the error when giving an estimate. Therefore, sampling method should provide not only a good estimate but also a valid sampling error.

Systematic sampling with one random start has been extensively used in forest surveys for its convenience in practice. Mathematical proofs indicate that such a sampling method is unbiased and efficient in most cases (Sukhatme, 1954; Gautschi, 1957). It is obvious that systematic sampling is consistent for the estimator will approach the parameter as the sample size increases. But systematic sampling does not provide sufficient information for computing sampling error exactly unless more than one random start is taken. The purpose of this paper is to discuss the advantages of systematic sampling with one random start and suggest a modification in order to provide a valid estimate of sampling error. A set of forest inventory data is used to show the efficiency of the systematic sample.

Three Basic Types of Sampling

Before we discuss systematic sampling, a brief description of the three basic sampling methods should be made: simple random, stratified random, and cluster sampling. All other sampling methods may be considered as equivalents or combinations of these three basic systems.

A *simple random sample* is selected from a population in such a way that (1) each individual in the population has the same chance of being selected as an element of the sample and (2) each element of the

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sample is selected from the population independently. The simple random sample provides a valid basis for computing the estimate and its sampling error. The estimate is unbiased, consistent and sufficient, but frequently inefficient.

In *stratified sampling* the population is divided into a number of strata and a random sample is drawn independently in each stratum. The estimate of the mean computed from the data of a stratified sample is unbiased and consistent. The efficiency of this sampling method depends upon the results of stratification. Since the sampling error of the estimated population mean is a function of the variance within the strata but not the variance of the original population, the estimate obtained from a stratified sample is efficient when stratification is made in such a way that a relatively homogeneous condition is obtained within each stratum.

In *cluster sampling*, the population is divided into a number of distinct and identifiable groups from which a simple random sample is drawn. The sampling unit, consisting of a certain number of individuals or elements of the population, is called a cluster. (Note that the sampling unit in the stratified sample is the individual or the element of the population). A cluster sample also provides a valid basis for computing the estimate of population mean and its sampling error. The estimate is unbiased and consistent. The efficiency of the estimate depends upon the variance between the clusters. Given a population with a fixed variance, maximizing the variation within the clusters will result in the smallest variance between clusters, and hence will give the most efficient estimate of the population mean.

In a forest survey, any forest may be considered as a population consisting of a number of arbitrarily divided areas which are treated as sampling units. When simple random sampling is used, the forest should be divided in such a way that the variation between unit areas is small. The use of old-time strip cruising with the strip across the gradient is an attempt to divide the forest into strips having more or less similarity. Each strip is an individual or element in the population and serves as a sampling unit. When a stratified sample is taken, the forest is first divided into a number of strata. Cover type, age-class, stocking level, or volume class may be used solely or in combination as the criterion for stratification. Strip cruising may also be considered as an efficient cluster sampling, with the strip as the cluster in which the variance is maximized by crossing the gradient.

Characteristics of Systematic Sample

Suppose a population consists of T individuals or elements serially numbered from 1 to T, and T is expressed as a product of two integers M and N, so that $T=M\times N$. Draw a random number less than N, say i, and select the individual with the corresponding serial number and every N-th individual in the population thereafter. The sample will contain the M individuals numbered as i, $i+N$, $i+2N$, ..., $i+(M-1)N$. This is called a systematic sample. A systematic sample has the following characteristics.

Cluster Sample in Nature

Systematic sampling strictly resembles cluster sampling (Sukhatme, 1954), a systematic sample being equivalent to a sample of one cluster selected out of the N clusters of M elements each shown in Table 1.

However, each cluster is no longer composed of a group of geographically adjacent elements. In forest surveys, a systematic sample is composed of a number of mechanically spaced sample plots which are distributed over the whole forest. Therefore, the systematic type of cluster sampling differs from the ordinary cluster sampling in the following respects.

Negative value of ρ. Sukhatme (1954) expressed the correlation coefficient among

TABLE 1. A schematic diagram of a population in the form of N columns of M elements each.

Sampling interval	Cluster No. 1	2	3	. . . .	i	. . . . .	N
1	1	2	3	. . . .	i	. . . . .	N
2	1+N	2+N	3+N	. . . .	i+N	. . . . .	2N
3	1+2N	2+2N	3+2N	. . . .	i+2N	. . . . .	3N
.	.	.	.	. . . .	.	. . . . .	.
.	.	.	.	. . . .	.	. . . . .	.
j	1+(j−1)N	.	.	. . . .	.	. . . . .	jN
.	.	.	.	. . . .	.	. . . . .	.
.	.	.	.	. . . .	.	. . . . .	.
M	1+(M−1)N	.	.	. . . .	i+(M−1)N	. . . . .	MN

elements in the same cluster, ρ, in terms of the variances between clusters, within clusters and of the total:

$$\rho = \frac{\frac{N-1}{N} S_b^2 - \frac{1}{M} S_w^2}{\frac{NM-1}{NM} S^2}$$

The relative efficiency of a cluster sampling is given by:

$$R.E. = \left[\frac{M(N-1)}{NM-1}\right]\left[\frac{1}{1+(M-1)\rho}\right]$$

When clusters are randomly formed, the expected value of S_w^2 and $M\,S_b^2$ will each be equal to S^2, then

$$\rho = \frac{1}{NM-1} \quad \text{and R. E.} = 1.$$

For ordinary cluster sampling, the elements in each cluster are geographically contiguous, hence ρ is usually positive and decreases as M increases, but the rate of decrease is small relative to the rate of increase in M. Thus an increase in the size of a cluster ordinarily leads to a substantial increase in the sampling variance of the sample estimate. As the clusters are formed by a systematic pattern, i.e. each cluster is composed of a group of mechanically spaced elements distributed evenly over the whole population, the variance within clusters, S_w^2, tends to be greater than that between clusters M S_b^2. These will give a negative value of ρ; thus the relative efficiency of systematic sampling is higher than simple random sampling.

Greater value of g. Smith (1938) proposed a relationship between the variance between clusters and the variance of the whole population as follows: $S_b^2 = S^2/M^g$ where M is the size of cluster, g is a constant. For ordinary cluster sampling, g is smaller than one. When the cluster is formed randomly, g is equal to one. For the systematic type of cluster sample, M S_b^2 tends to be smaller than S^2, then

$$M\ S_b^2 < S^2 \text{ or } S_b^2 < S^2/M$$

If we want to retain the relationship, $S_b^2 = S^2/M^g$, g must be greater than one.

Negative value of b. Jessen (1942) postulated that the variance within cluster is a monotonically increasing function of the size of cluster given by: $S_w^2 = a\ M^b$ where a and b are constants for a given population. For the ordinary cluster sample, b is positive. As for the systematic cluster, increasing cluster size leads to a decrease of variance within cluster and it approaches a limit of S^2 when M becomes the size of population. Obviously, b in this function will be negative.

Unbiased and Efficient Estimate of Population Mean

If the systematic sample is taken with a random start, the expected value of the sample mean is equal to the population mean. Therefore, a systematic sample with a random start provides an unbiased estimate of the population mean. The efficient estimator requires a small limiting variance or a small expected value of the sampling variance. The expected value of the sampling variance of the estimated population mean from a systematic sample generally is smaller than that from a simple random sample and stratified sample. This may vary with the types of parent population, however. According to the studies by Gautschi (1956) and Sukhatme (1954) the following conclusions can be reached.

Population in random order.

$EV_{sy} = EV_{st} = EV_{ra}$ where

EV_{sy} = Expected value of the sampling variance of the estimated population mean from a systematic sample with one random start,

EV_{st} = Expected value of the sampling variance of the estimated population mean from a stratified sample, and

EV_{ra} = Expected value of the sampling variance of the estimated population mean from a simple random sample.

Population with a linear trend.

$EV_{st} \leq EV_{sy} \leq EV_{ra}$

Population with serial correlation. If two elements X_i and X_j are positively correlated with a correlation which depends only on the "distance" $Z = |j-i|$ and which decreases as Z increases, then

$EV_{sy} \leq EV_{st} \leq EV_{ra}$

Population with periodic variation. The relative efficiency of systematic sampling for population showing periodic variation depends upon the choice of the interval between successive units sought to be included in the sample. If the interval coincides with the period of the cycle, the sample will contain units which are all alike; consequently, the relative increase in expected sampling variance of systematic sample over the random sample is maximum.

No Trustworthy Method for Estimating Sampling Variance from the Sample Data

The systematic sample with one random start does not provide sufficient information to compute exactly the sampling variance. Many approximate methods such as the overlapping-pair method (Hansen *et al.*, 1953), the balanced difference method (Yates, 1949), the method in which it is considered either as a stratified sample with one unit per stratum (Cochran, 1953), or as a simple random sample have been suggested for computing variance. The validity of such methods depends on (1) the satisfaction of the assumptions needed and (2) the type of population, which can not be predicted from the sample.

Osborne (1942) studied the sampling errors of cover type areas and concluded that treating a systematic sample as a simple or stratified random sample may lead to a very considerable over-estimate of the sampling error. DeLury (1950) gave an estimate of quantity and of the error of this estimate from a systematic sample by using the deviations from surface, fitted by means of orthogonal polynomials. Since the variation of a forest area generally differs from place to place, one of the assumptions underlying DeLury's method, namely constant variance, is vulnerable. Therefore, this method of computing the sampling error from a systematic sample has its limitation when applied to forest survey.

In summary, systematic samples are convenient to draw and to execute. They provide an unbiased, consistent and efficient estimate of the population mean when no coincidental periodicity is present, but they do not give enough information for computing an exact sampling variance when only one random start is employed.

Systematic Sample with Multiple Random Starts

From a population which has been systematically grouped into clusters (Table 1), several random numbers less than N are selected. The clusters with the corresponding selected random numbers are taken as the sample. Let the random numbers selected be i, j, and k for the case of three random starts; then the sample will include the individuals with the following series numbers:

random start no 1: i, i+N, i+2N, . . ., i+(M−1)N
random start no. 2: j, j+N, j+2N, . . ., j+(M−1)N
random start no. 3: k, k+N, k+2N, . . ., k+(M−1)N.

Such a sample is called a systematic sample with multiple (three) random starts. It resembles cluster sampling in which the variance within clusters has been maximized by distributing the elements of the cluster evenly over the population. In computing the estimates of population mean and sampling variance, each random start is treated as a cluster, and the conventional formulae for cluster sampling can be used. However, the binomial theory can not be used to find the sampling variance for proportions in a systematic sample with multiple random starts (Cochran, 1953).

Suppose that the M elements in any random start can be classified into two classes, say A and B, and that $P_i = a_i/M$ is the proportion in class A for the i-th random start. If a systematic sample with n random starts is taken, the average of observed p_i in the sample is used as the estimate of the population proportion p with sampling variance:

$$s_{\bar{p}}^2 = \left(\frac{N-n}{N}\right)\left(\frac{\sum_{i=1}^{n}(P_i-\bar{p})^2}{n(n-1)}\right)$$

where $(N-n)/N$ is the correction factor for the finite population.

One of the major problems is to determine how many random starts should be taken in order to obtain the most efficient result. The efficiency of the estimate of the population mean based on a small sample depends upon not only the standard error of the mean but also on the "t" value corresponding to the size of sample. A systematic sample with two and three random starts is required to use "t" values of 12.706 and 4.303 respectively in setting the confidence limits for a probability of 0.95 that confidence limits include the true mean. This means that it is necessary to reduce the standard error of mean to one-sixth of one-half of the value obtained by random sample in order to achieve the same confidence range. Hence, a fairly large number of random starts seems to be necessary.[1]

On the other hand, Gautschi (1957) found that systematic sampling with one random start is more precise than that with multiple random starts for population with serial correlation. In fact the systematic sample with one random start is spread more evenly through the population than the sample with multiple random starts which may contain elements very close together, giving about the same information. To increase the number of random starts will make the distribution of sampled elements approach the condition of a random sample and, consequently, reduce the efficiency of systematic sampling. Furthermore, the execution of systematic sampling becomes more complex in the forest as the number of random starts increases.

How the reduction of expected sampling variance compensates the loss due to higher t-value in a multiple-random-start systematic sample is not a simple question to answer, since the rate of reducing the expected sampling variance as the size of systematic cluster increases, changes with the type of population sampled. In general, the number of random starts should not exceed the point at which the change of

[1]The consideration of "t" value in setting confidence limits for the small size sample was brought to the author's attention by J. G. Osborne, U. S. Forest Service.

t-value with the increase of one degree of freedom is small. Probably five or six random starts are the minimum in order to avoid the high t-value when computing the confidence interval. Actually, the multiple-random-start systematic sample has its great merit when being used in a two-stage or stratified sampling procedure.

For instance, one can either take a simple random sample or stratify the population first; within each unit sampled or stratum a two- or three-random-start systematic sample is taken. If the number of the first stage samples or the number of strata is more than ten, the final confidence interval will be computed with a t-value corresponding to fairly large degrees of freedom and a small expected standard error. If one wants to use the optimum allocation in a stratified sample, the number of elements in each random start can be adjusted in order to increase the flexibility in deciding upon the sampling intensity.

In ordinary cluster sampling, increase of cluster size will lead to loss of precision but help to reduce the cost of sampling. Since the systematic cluster is composed of elements evenly distributed over the whole population, increase of the size of cluster may not reduce the cost if the sampling intensity remains the same by adjusting the number of random starts. Therefore, to determine the optimum size of cluster which will provide the maximum information for the funds available is a problem of minimizing the variance of the estimated cluster mean by choosing a suitable M (size of cluster) and n (number of clusters) in the sample with a side condition, $nM = C$ (constant) = (funds available)/(cost per sampling unit).

From Jessen's formula $S_w = a M^b$, Sukhatme (1954) obtained: sampling variance for the cluster mean,

$$V = \frac{1}{n}[S^2 - (M-1)\, a\, M^{b-1}] \quad \ldots (1)$$

where, S^2, a and b are constants for a given population.

To minimize V by the Lagrange-multiplier-method (Kaplan, 1952), we have

$$\frac{\partial V}{\partial M} = -\frac{1}{n}[abM^{b-1} - a(b-1)M^{b-2}] \quad \ldots (2)$$

$$\frac{\partial V}{\partial n} = -\frac{1}{n^2}[S^2 - (M-1)aM^{b-1}] = -\frac{1}{n}V \quad \ldots (3)$$

Let $h(n,M) = nM - C = O$, then $\frac{\partial h}{\partial M} = n$, and $\frac{\partial h}{\partial n} = M$, we form a set of equations:

$$\frac{\partial V}{\partial M} + \lambda n = O \quad \ldots (4)$$

$$\frac{\partial V}{\partial n} + \lambda M = O \quad \ldots (5)$$

$$nM - C = O \quad \ldots (6)$$

On eliminating λ from (4) and (5),

$$-\left(\frac{\partial V}{\partial M}\right)\left(\frac{M}{V}\right) = 1 \quad \ldots (7)$$

Substituting (1) and (2) in (7) and simplifying,

$$M^b[1 + b\,(1 - 1/M)] = S^2/a \quad \ldots (8)$$

In the systematic cluster sampling, M is usually large, and (8) can be further simplified:

$$M^b \doteq S^2/[a(1+b)] \quad \ldots (9)$$

Finally, we have

$$\log M \doteq \frac{1}{b}[\log S^2 - \log a - \log(1+b)] \quad \ldots (10)$$

Assuming Jessen's formula holds good, a systematic sample will have the smallest sampling variance for a given population when M is defined as (10).

Illustration

Data from a 100 percent cruise of a 40-acre tract of old-growth Douglas-fir timber

reported by Johnson and Hixon (1952) were used here to demonstrate the precision of systematic sampling. The original data were shown with 1,600 units of $^1/_{40}$-acre each. These units were geographically grouped into 400 $^1/_{10}$-acre plots which compose a parent population to be sampled. Suppose these 400 plots, 20 rows by 20 columns, are further grouped geographically into 16 blocks (4 rows by 4 columns), each block consisting of 25 plots and constituting a stratum. If we give a series number from 1 to 25 to each of the plots of the 16 blocks, following a certain systematic pattern, all plots having the same series number form a systematic cluster. In other words, the parent population is systematically grouped into 25 clusters; each cluster contains 16 plots, one from each of the 16 blocks. Table 2 shows the formation of clusters and strata of the 40-acre timber tract.

First, considering the population as being geographically stratified, an analysis of variance will give the expected sampling variance and the relative efficiency of a stratified sample as compared with a simple random sample (Table 3).

Second, by treating the population as an aggregate of systematically-formed clusters, the reduction of sampling variance is shown in Table 4.

When a systematic sample is taken from this timber tract with a sampling intensity of .04, i.e. randomly select one cluster from the 25 systematic clusters; the expected sampling variance is 308,598. By treating the systematic sample as a simple random sample and a stratified sample, the sampling variance will be increased to 804,835 and 717,327 respectively. Therefore, the function of a systematic sample in minimizing the sampling variance will be lost by treating as either a simple random sample or a

TABLE 2. Stratification and cluster-formation of the parent population.

Block or stratum number	Cluster number or plot number in each block																							
	1		2									j												25
1	$X_{1.1}$		$X_{1.2}$									$X_{1.j}$												$X_{1.25}$
2	$X_{2.1}$		$X_{2.2}$									$X_{2.j}$												$X_{2.25}$
.	.		.									.												.
.	.		.									.												.
i	$X_{i.1}$		$X_{i.2}$									$X_{i.j}$												$X_{i.25}$
.	.		.									.												.
.	.		.									.												.
16	$X_{16.1}$		$X_{16.2}$									$X_{16.j}$												$X_{16.25}$

TABLE 3. Analysis of variance of geographically stratified population.[1]

Source of variance	D. F.	S. S.	Variance
Between strata	15	45,677,623	3,045,175
Within strata	384	275,451,585	717,321
Total	399	321,129,208	804,835

[1]Relative efficiency $= \frac{\text{Expected sampling variance for a simple random sample}}{\text{Expected sampling variance for a stratified sample}}$

$= \frac{\text{Variance of total}}{\text{Variance within strata}} = \frac{804,835}{717,327} = 1.220$

TABLE 4. Analysis of variance of population composed of systematic clusters.[1]

Source of variance	D. F.	S. S.	Variance
Between clusters	24	7,406,351	308,598
Within clusters	375	313,722,857	836,611
Total	399	321,129,208	804,835

[1]Relative efficiency $= \frac{\text{Expected sampling variance for a simple random sample}}{\text{Expected sampling variance for a systematic cluster sample}}$

$= \frac{\text{Variance of total}}{\text{Variance between clusters}} = \frac{804,835}{308,598} = 2.608$

TABLE 5. The expected sampling variance and relative efficiency of systematic cluster sampling and geographically stratified sampling for an old-growth Douglas-fir tract under different patterns of grouping.

No. of clusters or size of stratum	Size of cluster or no. of strata	Systematic cluster sample			Geographically stratified sample		
		Expected sampling variance	Variance within clusters	Relative efficiency[1]	Variance between strata	Expected sampling variance	Relative efficiency[2]
N	M	MS_b^2	S_w^2		NS_b^2	S_w^2	
8	50	385,527	812,322	2.088	1,294,202	736,324	1.093
10	40	200,213	818,788	4.020	1,568,869	722,065	1.115
16	25	549,014	814,828	1.466	2,138,845	719,458	1.190
20	20	201,872	834,983	3.987	2,819,536	704,100	1.431
25	16	308,598	836,611	2.608	3,045,175	717,321	1.220
40	10	340,482	855,140	2.364	4,540,615	718,625	1.120
50	8	405,739	860,679	1.984	4,558,054	737,974	1.091

[1]Relative efficiency $= S^2/MS_b^2$, where $S^2 = 804, 835$.

[2]Relative efficiency $= S^2/S_w^2$.

stratified sample. The exact sampling variance for a systematic sample, however, can be obtained only by taking multiple random starts.

By changing the size of blocks to 8, 10, 16, 20, 40 and 50 units respectively, the expected sampling variance and relative efficiency for stratified sample and systematic cluster sample have been computed through analysis of variance and listed in Table 5. The over-estimate of sampling variance by treating the systematic sample as a simple or stratified random sample is true for all the patterns used for grouping.

By applying Sukhatme's and Smith's formulae respectively, ρ (correlation coefficient between plots in the same systematic cluster) and g have been computed for different sizes of cluster. Table 6 supports the conclusions that the correlation coefficient between plots in the same systematic cluster is negative and the g value is greater than one.

From data in Table 5, the constants a and b in Jessen's formula are estimated for this population by the least squares method. They are 918,400 and -0.0325 respectively.

TABLE 6. The correlation coefficient ρ and g of systematic cluster sample of different sizes.

Size of systematic cluster	ρ	g
50	-0.012	2.719
40	-0.020	3.001
25	-0.015	3.005
20	-0.040	3.461
16	-0.042	3.506
10	-0.065	3.975
8	-0.072	4.209

Conclusions

Systematic sampling with one random start resembles cluster sampling with one cluster only, in which the cluster consists of a number of elements distributed evenly over the whole population. Such systematic cluster sample provides an unbiased, consistent and efficient estimate of the population mean. However, there has not been any exact method to compute the sampling variance from a systematic sample with only one random start. Treating a systematic sample as a simple random or stratified sample results in an overestimate of sampling variance. A modified method by which the most of the advantage of systematic sampling can be achieved would be very useful. If multiple random starts are taken, the systematic sample represents a cluster sample with several clusters. Exact estimates of the sampling variance are possible. A systematic sample, therefore, will provide good estimates regardless of the type of population. In addition, systematic sampling with multiple random starts is not much more complicated in forestry practice than that with one random start only. Therefore, it is highly applicable in forest surveys and even in many cases of forest economics research.

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Sequential Sampling in Spruce Budworm Control Projects

BY
WALTER E. COLE

DETERMINING the success of past aerial spray projects for the control of the spruce budworm, *Choristoneura fumiferana* (Clem.), required extensive sampling. This sampling conducted prior to and after the application of the spray was designed to evaluate the effect of the spray on reducing the budworm larval population and was expressed in percent mortality.

Sampling was based upon plots located systematically along a compass line. The prespray larval count was obtained by counting the number of larvae on each of two 15-inch twigs from each of 5 trees per plot from each of 10 plots spaced 5 chains apart, or 100 twigs. The postspray larval count was based on twice the number of twigs taken (or 4 twigs) from the same trees, or 200 twigs. The percent mortality was then calculated by using the following formula (Whiteside *et al.*, 1956):

$$\text{Percent mortality} = 100 \times \frac{\text{Prespray larval count} \times 2 - \text{postspray larval count}}{\text{Prespray larval count} \times 2}$$

In the majority of spray operations to date, only one "mortality line" could be run in a particular spray block consisting of 3,000 to 8,000 acres because of limitations of time. Consequently, the estimate of mortality of larvae for a spray block has been based entirely on one mortality line. No variances have been computed, therefore, and thus no estimates of the confidence levels obtained.

Advances in survey techniques, such as the sequential plan described here, should result in improved analyses of population reduction by aerial spraying. For large-scale control projects it is desirable to have a rapid, reliable method of classifying larval populations. Broad classifications such as light, medium, and heavy infestations have been generally accepted. Also, it is desirable to evaluate the results of a spray project as reliably as possible. Lacking better information, the attainment of 95 percent or greater reduction in the larval population has been termed successful.

The sequential plan, while having no fixed sample size, permits the classification of the pre- and postcontrol populations within specified limits of accuracy. The precontrol sampling is simply a method of appraisal survey and need be done only to determine the precontrol population level to decide whether control is justified or not. Actually only a postcontrol sample is needed to determine the effectiveness of a spray project. Regardless of the original larval concentration, the final population level is, of course, the primary concern in control.

The Sequential Plan for Precontrol Sampling or Appraisal Survey

Certain basic knowledge of the insect is required to develop a sequential plan for

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sampling budworm larval populations. The type of frequency distribution must be determined since this governs which formula will be used. Sufficient information must be available on the number of insects per sampling unit to set meaningful class limits or degrees of infestations.

The particular sequential formulae for the more common types of distributions have been provided by Oakland (1950, 1951) for the negative binomial and the binomial distributions, by Stark (1952) for the normal, and by Morris (1954, 1955) for the negative binomial. Waters (1955) provided a review of the formulae for these types of distributions, including the Poisson.

Budworm larval populations conform to the negative binomial, $(q-p)^{-k}$, (Morris, 1954; Waters, 1955). In the theoretical negative binomial distribution the variance, s^2, is usually greater than the mean, $\bar{x}$, but does not increase proportionally. This can be tested graphically for an observed series by plotting the variances and the means for different sets of data. The variance of an observed negative binomial distribution can be represented as $s^2 = \bar{x} + (\bar{x}^2/k)$, where $\bar{x}$ is the mean and k is a constant. However, as k may be calculated directly by several methods, differing in efficiency according to circumstances, slight departures from the relationship may occur. Anscombe (1949) presents methods of estimating and testing k, but the method used in this paper is that of Bliss and Owen as reported by Waters (1955). The main difference between Waters' work and what is reported in this paper is that Waters presented a theoretical basis for sequential sampling, whereas this paper reports results of trials of sequential sampling under field conditions of a large scale spruce budworm control project.

In this paper class limits are established for determining light, medium, and heavy populations by using the average number of insects per sampling unit, i.e., a 15-inch twig taken at mid-crown of Douglas-fir. These class limits were determined by a general correlation between the average number of larvae and percent defoliation per twig as found during the budworm population-damage study in southern Idaho. These class limits may not be applicable in other areas nor for other tree species than Douglas-fir. The data used in this paper were gathered from 3- to 5-year-old budworm infestations on young Douglas-fir trees 10 to 12 inches in diameter and averaging 60 feet in height.

The class limits are as follows:

To distinguish between Class I (light) and Class II (medium) infestations:

M_0—that the average number of larvae per 15-inch twig is 2.0 or fewer (Class I).

M_1—that the average number of larvae per 15-inch twig is 3.0 or more (Class II).

To distinguish between Class II (medium) and Class III (heavy) infestations:

M_0—that the average number of larvae per 15-inch twig is 5.0 or fewer (Class II).

M_1—that the average number of larvae per 15-inch twig is 6.0 or more (Class III).

The values of the distribution constants are shown in Table 1.

Two conventional types of error are involved with each set of standards (M_0 and M_1). Type I rejects a standard when in fact it is true, and Type II accepts a standard when in fact it is false. For this sampling plan the risk of either of these two errors occurring has been set at 10 percent and labeled α and β. Thus, the probability is one-tenth that a stand may be classified incorrectly.

The acceptance and rejection lines. The sequential plan utilizes one or more pairs of lines (Fig. 1), depending on the number of classes which are to be distinguished.

The lines are computed as follows:

$$d_0 = sn + h_0 \text{ (lower line)}$$
$$d_1 = sn + h_1 \text{ (upper line)}$$

TABLE 1. Values of the distribution constants under the alternate standards.

Constant	Infestation			
	Light (M_o)	Medium (M_1)	Medium (M_o)	Heavy (M_1)
Mean = kp	$kp_o = 2$	$kp_1 = 3$	$kp_o = 5$	$kp_1 = 6$
p = kp/k	$p_o = 0.258$	$p_1 = 0.388$	$p_o = 0.646$	$p_1 = 0.775$
q = p + 1	$q_o = 1.258$	$q_1 = 1.388$	$q_o = 1.646$	$q_1 = 1.775$
Var. = kpq	var. = 2.516	var. = 4.164	var. = 8.230	var. = 10.650

where d = cumulative number of insects

n = the number of sampling units examined

s = the slope of the line

h_o and h_1 = the intercepts.

For a k of 7.736, computed in this case,

$$s = k\frac{\log (q_1/q_o)}{\log (p_1q_o/p_oq_1)} = 2.456$$

and h_o and h_1 are computed as follows:

$$h_o = \frac{\log B}{\log (p_1q_o/p_oq_1)} = -7.095$$

$$\text{and } h_1 = \frac{\log A}{\log (p_1q_o/p_oq_1)} = 7.095$$

$$\text{where } B = \frac{\beta}{1-\alpha}$$

$$\text{and } A = \frac{1-\beta}{\alpha}$$

In application, accept M_o if $d \leq 2.456n - 7.095$ and accept M_1 if $d \geq 2.456n + 7.095$.

These lines, as well as the ones to distinguish Class II from Class III infestations, are shown in Figure 1.

The operating characteristic curves. The operating characteristic curves (Fig. 2) show the probability, L(kp), of accepting M_o for any possible level of the population mean. When the mean, kp, is 2.0, the probability of accepting M_o (Class I) is 0.90 (Fig. 2, left-hand curve); hence the probability of accepting M_1 (Class II) is 0.10. When kp is 3.0, L(kp) is 0.10 for accepting M_o (Class I) and 0.90 for accepting M_1 (Class II).

As kp decreases below 2.0, L(kp) for M_o becomes very high and as it increases above 3.0, L(kp) for M_o becomes very low. By the same measure at a kp of approximately 2.4 the chances of accepting M_o and M_1 are equal. The right-hand curve (Fig. 2) may be used in the same manner for Class II versus Class III.

The operating characteristic curves are calculated from

$$L(kp) = \frac{A^h - 1}{A^h - B^h} \text{ with A and B}$$

as defined previously and

$$p = \frac{1-(q_o/q_1)^h}{(p_1q_o/p_oq_1)^h - 1}$$

where h is a "dummy variable" which may be assigned convenient values.

The average sample number curve. The average sample number curves (Fig. 3) make it possible to determine mean number of twigs, E(n), that will be measured to reach a decision at any population level. The peaks of the curves occur where populations are borderline cases between the different classes. At population levels where kp is definitely within a class, fewer twigs need be sampled. However, E(n) is the average sample number and may or may not be exceeded on any particular line of plots.

For the different values of kp, E(n) is calculated from

$$En = \frac{h_1 + (h_o - h_1)L(kp)}{kp - s}$$

where h_o, h_1, and s have already been calculated for the acceptance and rejection lines.

The Sequential Plan for Postcontrol Sampling

In order to rate the success of the past control projects, Whiteside *et al.* (1956) set standards as follows:

"Excellent control (97-100%): project average should fall in this range.

Good control (95-97%): acceptable for blocks and occasional units.

Marginal control (90-94%): acceptable for occasional blocks but not for units.

Poor control (below 90%): unsatisfactory, respraying probably necessary."

During a special meeting on spruce budworm problems in the West, held at Spokane, Washington, on November 30, 1955, representatives of budworm control projects concluded that the kill should average 97 to 98 percent and that the effectiveness of

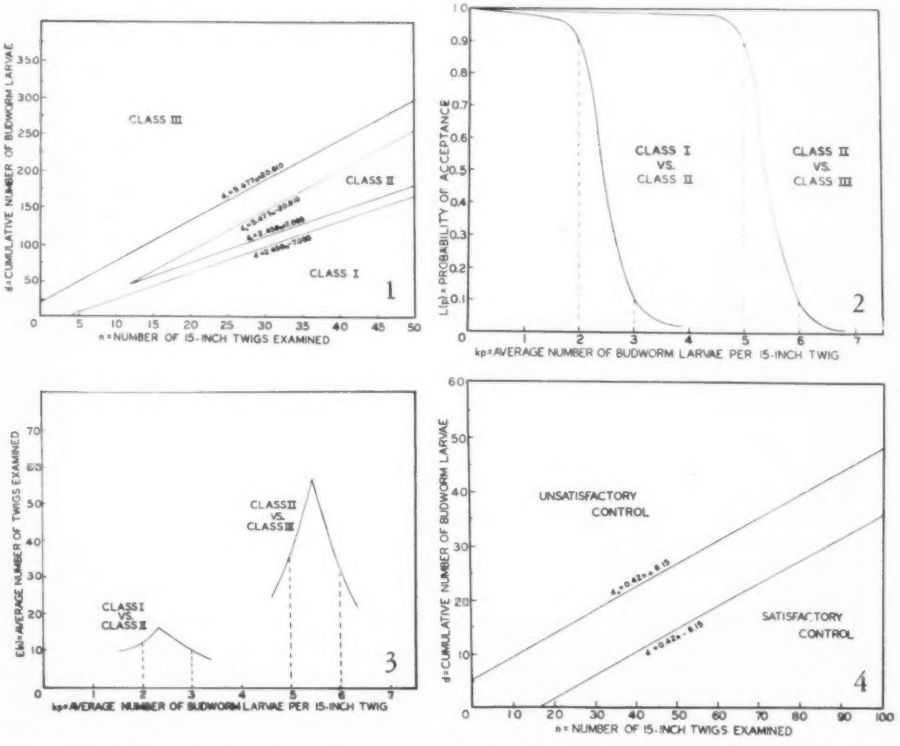

d = CUMULATIVE NUMBER OF BUDWORM LARVAE
CLASS III
CLASS II
CLASS I
1
n = NUMBER OF 15-INCH TWIGS EXAMINED
L(p) = PROBABILITY OF ACCEPTANCE
CLASS I VS. CLASS II
CLASS II VS. CLASS III
2
kp = AVERAGE NUMBER OF BUDWORM LARVAE PER 15-INCH TWIG
E(n) = AVERAGE NUMBER OF TWIGS EXAMINED
CLASS II VS. CLASS III
CLASS I VS. CLASS II
3
kp = AVERAGE NUMBER OF BUDWORM LARVAE PER 15-INCH TWIG
d = CUMULATIVE NUMBER OF BUDWORM LARVAE
UNSATISFACTORY CONTROL
SATISFACTORY CONTROL
4
n = NUMBER OF 15-INCH TWIGS EXAMINED

FIGURE 1. *Sequential graph for precontrol sampling of spruce budworm larval populations.* FIGURE 2. *Operating characteristic curves of the sequential plan for precontrol sampling of spruce budworm larval populations.* FIGURE 3. *The average sampling number curves of the sequential plan for precontrol sampling of spruce budworm larval populations.* FIGURE 4. *Sequential graph for postcontrol sampling of spruce budworm larval populations.*

a kill of 85 to 95 percent is not known. Consequently, 95-percent reduction was used in setting the class limits for the following sampling procedure. Postcontrol population data, gathered on control projects in southern Idaho during the past 3 years, were tested and found to follow a Poisson-like distribution. The Poisson is described by just one parameter, the mean. The variance is equal to the mean at all population levels.

Postcontrol sampling should reveal whether satisfactory or unsatisfactory reduction of the larval population resulted from spraying. The following standard was set up, using the average number of insects per sampling unit as the class limits.

To distinguish between satisfactory and unsatisfactory control

M_o—that the average number of larvae per 15-inch twig is 0.35 or fewer (satisfactory)

M_1—that the average number of larvae per 15-inch twig is 0.50 or more (unsatisfactory).

These class limits were determined by using the 95-percent reduction of a Class III (heavy) infestation. The 95-percent reduction level of a Class III infestation also should be, in terms of larvae per twig, acceptable for Class I and Class II infestations.

The values are then calculated. The methods and formulae for this were provided by Oakland (1950) and Waters (1955).

Again, the two types of errors are involved and a confidence level of 90 percent used.

The formulae for the decision lines are

$$d_o = sn - h_o$$
$$\text{and } d_1 = sn + h_1.$$

Where d is the cumulative number of insects, n is the number of sampling units examined, s is the slope, h_o and h_1 the intercepts, and m_o and m_1 the mean number of larvae per 15-inch twig for their respective standards.

To solve for s

$$s = \frac{m_1 - m_o}{\log_e m_1 - \log_e m_o} = 0.42.$$

To solve for h_o and h_1

$$h_o = \frac{\log_e \frac{1-\alpha}{\beta}}{\log_e m_1 - \log_e m_o} = 6.15,$$

and

$$h_1 = \frac{\log_e \frac{1-\beta}{\alpha}}{\log_e m_1 - \log_e m_o} = 6.15$$

where $\alpha = \beta = 0.10$.
Accept M_o if $d \leq 0.42n - 6.15$.
Accept M_1 if $d \geq 0.42n + 6.15$.

These lines are plotted as shown in Figure 4.

The probability, L(m), of accepting M_o and M_1 for any possible population level is shown in the operating characteristic curve (Fig. 5). Since $\alpha = \beta$ and $h_o = h_1$, m is found by

$$m = \frac{\frac{s}{h} - \log_e \frac{L(m)}{1-L(m)}}{\frac{\left(L(m)\right)^{\frac{1}{h}}}{(1-L(m))} - 1}.$$

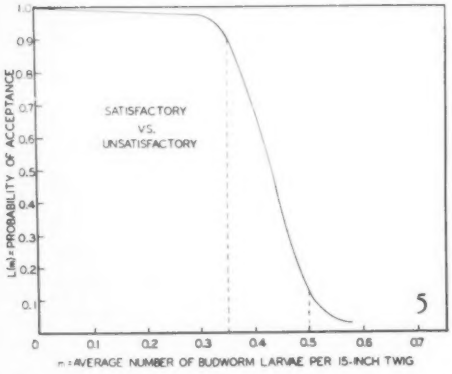
The average sample number curve (Fig. 6) was calculated from the following formula for the different values of m

$$E(n) = \frac{L(m)(h_o + h_1) - h_1}{s - m}$$

Both the OC and ASN curves operate in the same manner as in the precontrol sampling.

Application of the Plan

In previous years sampling of budworm populations during control projects to determine mortality has involved much effort with limited reliability. Because of the time required to run the lines, less than the ma-



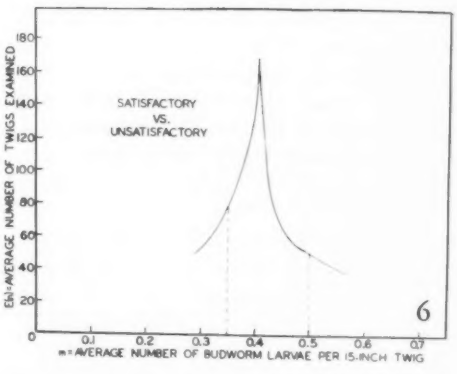


FIGURE 5. *Operating characteristic curve of the sequential plan for postcontrol sampling of spruce budworm larval populations.* FIGURE 6. *The average sample number curve of the sequential plan for postcontrol sampling of spruce budworm larval populations.*

jority of spray blocks could be sampled. During the 1957 Spruce Budworm Control Project in southern Idaho the sequential plan was utilized. As a result, 83 percent of the spray blocks were sampled for larval survival as compared with 53 and 68 percent sampled for larval mortality in other years (Table 2), yet there was no corresponding increase in the field crew. This is particularly impressive because 542,267 of the 660,632 acres sprayed were within the Idaho Wilderness Area, and travel was limited to horse or foot.

The time saving effected by the sequential plan is probably its greatest advantage. No time is wasted in superfluous sampling where the infestation falls distinctly into a class. The main disadvantage in sequential sampling is that increased sampling is required when the infestation is halfway between the borderlines of classification. However, an upper limit can be set for a sample line—50 twigs in precontrol, and 100 twigs in postcontrol sampling. If the cumulative number of larvae still falls between a set of bands, the infestation may be called "light to medium" or "medium to heavy" in precontrol sampling or "equal to 95-percent reduction" in postcontrol sampling.

The sample lines established in 1957 (Table 2) were, by nature of the sequential plan, considerably shorter in length than the fixed sample lines used in previous projects. However, a line in either case constituted a sample, and so the number of

TABLE 2. Personnel, acreage, and percent sampling in control projects in southern Idaho.

Year	Ground personnel	Acreage sprayed	Acres per person	Number sample lines established	Lines per person	Percent of spray blocks sampled
1955	33	893,214	27,067	58	1.45	53
1956	35	475,901	13,597	70	2.00	68
1957	26	660,632	25,409	107	4.12	83

samples obtained was greatly increased. Whether the increase in samples is placed within single spray blocks or more spray blocks are sampled is determined by the natural variation found within and between blocks. The sampling intensity applied in a project depends, of course, upon the available personnel and time.

If adequate information has been obtained on the current budworm population by egg samples, samples of overwintering larvae, or checks of the population entering the needles and buds, only post control sampling is needed to determine the effectiveness of a spray project. That is, when using the sequential plan, only the postcontrol sampling is needed to evaluate the residual population level.

Precontrol sampling was done in 1957 to increase the basic data and further refine the sequential plan as shown in this report. As a result, a new sequential plan was devised for future projects. The actual sampling progresses similarly to the past method. If a precontrol sample is desirable, a sample line is established prior to spraying by a compass course running perpendicular to the proposed spray swath or across contours in what is considered to be a representative portion of the block. Sample plots are regularly spaced along this cruise line so that more than one spray swath will be sampled. The line may be "strung in" with marking twine and the sampled trees tagged for ease of postcontrol sampling.

In the past selected cruise lines and evenly spaced plots have been commonly used and no sampling error was computed. If sampling accuracy is to be expressed, as in the sequential plan, then strict adherence to proper sampling methods would require a random location of cruise lines and of plots along the line. Data for this study were not collected in a random manner, but it is felt that they do represent a good measure of the variation of each block because of the representative manner in which they were collected. In future use of the sequential plan for evaluating budworm control, cruise lines should be selected with care to insure representativeness of sampling, or else the lines and plots should be randomly selected. This latter method has not been fully explored to determine the magnitude of variation that might be encountered, and the number of randomly selected lines and plots that would be required in postcontrol evaluations. This phase of the problem warrants further study.

At each plot five 15-inch twigs from each tree are taken; the number of larvae is counted and plotted on the graph (Fig. 1). The plotted points must fall outside the band before the degree of infestation is defined. Table 3 shows these lines for convenient field use.

For example, suppose 5 twigs are sampled and 20 larvae are found. The number 20 is then plotted over twig 5; in this position it is between both sets of bands. Since both Class II and Class III are being tested these results lie in the band of nondecision between these classes. Actually no decision is possible until at least 10 twigs have been examined and only then if the results are to throw the infestation into Class I or Class III. At least 15 twigs will have to be examined before Class II could be accepted at the expense of both Class I and Class III. Five more twigs are sampled, and 15 larvae are found. The cumulative number is now 35 larvae over 10 twigs. After plotting, this total is still between both sets of bands. Sampling continues until the point falls outside the bands. In this case, at 25 twigs the cumulative number of larvae is 97. The point now falls in the Class II zone and the sample is identified as a Class II infestation. By this means the precontrol budworm larvae population can be defined as Class I, II, or III.

Ten days after spraying, the tagged trees should be resampled in the above manner, except that the postcontrol sequential table (Table 4) should be employed. This sampling operates in the same manner as the precontrol sampling, i.e., by plotting the cumulative number of larvae per 15-inch twig over the number of twigs ex-

TABLE 3. Sequential table for field use in precontrol sampling of spruce budworm larval populations.

Number of twigs examined	Cumulative number of budworm larvae							
	Class I	vs.	Class II		Class II	vs.	Class III	
5	5		19		7		48	
10	17		32		34		75	
15	30		44		62		103	
20	42		56		89		130	
25	54		68		116		158	
30	67		81		144		185	
35	79		93		171		212	
40	91		105		198		240	
45	103		118		226		267	
50	116		130		253		294	
	CLASS I	Continue sampling		CLASS II		Continue sampling		CLASS III

amined until the plotted point falls outside of the bands.

Table 4 shows these lines for convenient field use.

It is suggested that at the end of each sequential sampling line the worker off-set from one-fourth to one-half mile and continue upslope with a second sample line in the same direction. If, however, the higher elevations have not been released for spraying, or have been sprayed, the worker should off-set and reverse his direction of travel.

If, as suggested above, only a postcontrol sample is to be used to determine residual population rather than percentage reduction, no resampling is involved. Ten days after spraying, cruise lines are selected and twigs gathered as previously described. This 10-day waiting period is necessary to allow maximum mortality to occur.

TABLE 4. Sequential table for field use in postcontrol sampling of spruce budworm larval populations.

Number of twigs examined	Cumulative number of budworm larvae		
	Satisfactory vs. Unsatisfactory		
15	–		12
20	2		14
25	4		17
30	6		19
35	8		21
40	11		23
45	13		25
50	15		27
55	17		29
60	19		31
65	21		34
70	24		36
75	26		38
80	28		40
85	30		42
90	32		44
95	34		46
100	36		48
	Satisfactory Control	Continue sampling	Unsatisfactory Control

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Conifers: South African Methods of Cultivation

By W. E. Hiley. Faber & Faber, 24 Russell Square, London W.C.1. 123 pp. 21 s. ($2.95). 1959.

Review by Stephen H. Spurr
The University of Michigan

Few recent developments in silviculture have been so stimulating or intriguing as the heavy thinning and pruning techniques used in South Africa to grow exotic pines to large sizes in short rotations. The evaluation of these techniques by a leading English forester in a short, technically competent, and very readable book will be of major interest to American foresters, particularly those in the southern pine and Douglas-fir regions.

W. E. Hiley is widely known both for his own books (Economics of forestry, Improvement of woodlands, Woodland management, and Economics of plantations) and for his own practical estate management. He has been long interested in the silvicultural techniques pioneered by Ian Craib in South Africa, and the present book is an outgrowth of a second study tour after a ten-year interval through the exotic pine plantations of South Africa.

South Africa is a timber-importing region whose indigenous forests are few and badly depleted. Yet, in at least two regions, nonforested areas highly suitable for tree growth occur. Along the south coast of Cape Province, the rainfall is fairly evenly distributed throughout the year or occurs principally in winter. Here, *Pinus pinaster* (Maritime pine), *Pinus radiata* (Monterey pine), and *Pinus canariensis* (Canary Island pine) have been widely planted. Pinaster of Portuguese seed origin is the chief timber tree, growing where the rainfall is only 20-25 inches, and capable of standing quite severe frosts and of growing on relatively poor soil.

It is, however, with the newer plantations in the highlands of the Drakensberg Mountains in western Natal, Swaziland, and eastern Transvaal that Hiley is more concerned. Here, at elevations of from 4,000 to 6,500 feet, extensive plantations of *Pinus patula* (a Mexican species) and *Pinus elliottii* (termed *caribaea* in South African literature) have been established in the last few decades.

As of 1955, there were about 433,000 acres of state conifer plantations in South Africa (chiefly patula, caribaea, and pinaster in that order). A greater acreage (1,387,000 acres) has been planted by private and communal enterprise.

Plantation forestry in South Africa is a profitable business because of the availability of good sites, cheap labor, and good markets. Only the better sites are planted. Patula

reaches a height of 44 feet in 10 years from planting (11 from seed) and an average volume of 2500 cubic feet outside bark. At 20 years, the average height is 75 feet and the volume about 6,000 cubic feet. Radiata is even more rapidly growing, while pinaster and caribaea are somewhat slower in development. All, however, fall off sharply in growth with time, and are managed on short rotations of from 30 years on first-quality sites to 50 years on third-quality.

The silviculture is intensive. With native labor costing only a little more than 4 shillings (56 cents) for a minimum amount of work per day, agricultural techniques are feasible. The seedlings are transplanted in the nursery and planted out when 10-14 months old and 9 inches high with soil attached to the roots. The planting site is usually completely plowed. Planting is exactly at 9 x 9 foot intervals; the 10 to 20 percent of the trees that die are promptly replaced, and the plantations are weeded as necessary to reduce grass competition, on the average twice in each of the first two years.

An intensive and formal thinning schedule is followed, aimed at reducing competition between trees to a minimum throughout the rotation so as to achieve the maximum possible diameter growth. For patula on the best sites, the original 530 stems per acre are reduced to exactly 300 at 8 years, 200 at 12 years, 130 at 18 years and, if needed, to 100 at 25 years. As the stand develops, all trees are pruned. Patula, for instance, is pruned to 7 feet, 5 or 6 years after planting when the trees are about 20 feet high, 15 feet when the trees are 30 feet high, 22 feet when the trees are 40 feet high and sometimes to 36 feet when the trees are 55 feet high. The pruning is designed to provide clear wood in the butt log and tight knots in the upper logs.

The experimental thinning plots, termed Correlated Curve Trend (C.C.T.) are equally rigorous and formal. Beginning with a 6 x 6 plantation, plots are progressively thinned down from 1200 to 600, 400, 300, 200, 150, 100 and 50 stems per acre, each thinning being scheduled as soon as comparable trees in the next denser plot drop behind those on the thinned plots by 0.1 inch, this being considered to be the point where competition has commenced. The first thinnings may be scheduled at two years from planting and the lowest density of 50 stems per acre may be reached by 8 years.

Hiley paints a picture of intensive agricultural plantation techniques being applied vigorously and successfully to the growing of conifer sawlogs. The silvicultural techniques differ markedly from the classical ones of western Europe, yet appear to be justified by the results achieved. At the same time, the new system has become quite rigid and formal. "Deviationists are discouraged and it is rather too easy to follow the official line." The brief and well-written evaluation of this system by an eminent outside expert will undoubtedly stimulate all silviculturists to a fresh appraisal of their own problems.

Variations in Moisture Contents Of Dormant Buds

BY
THEODORE T. KOZLOWSKI
ALICE E. PETERSEN

CHANGES IN MOISTURE CONTENTS of various plant tissues over a short time period may result from excess transpiration over absorption, internal moisture redistributions, absorption of water from the atmosphere, and from a combination of these (Kramer, 1949, 1956). Wilson, Boggess and Kramer (1953) observed that water content of leaves, stems and roots of sunflower decreased during the day and increased during the night. The decreases were attributed to high transpiration which caused withdrawal of water from the stems and roots more rapidly than water could be absorbed. Diurnal shrinkage of fruits as a result of water loss to other tissues has been observed in lemons (Bartholomew, 1926), apples (Magness, Degman and Furr, 1935), and oranges (Coit and Hodgson, 1919; Rokach, 1953). Rokach (1953) reported that water was easily transported from an orange on a defoliated main branch to a leafy lateral branch. The observation that older leaves often are the first to wilt during droughts provides additional evidence of internal moisture stress and redistribution (Kramer, 1949).

Preliminary experiments performed on dormant buds of American elm (*Ulmus americana* L.), horsechestnut (*Aesculus hippocastanum* L.) and eastern white pine (*Pinus strobus* L.) trees in full leaf indicated that moisture contents of dormant buds varied considerably during the day. Additional experiments were performed to investigate the amount of short-time variation in moisture contents of dormant buds and the possible causes of such changes. This study was conducted in Amherst, Massachusetts.

Methods

Attached buds. An experiment was performed to test the effects of time of day, height of sampling, and exposure on moisture contents of dormant eastern white pine buds. Samples each consisting of 15 terminal buds were removed from a white pine tree 10.5 ft high. Samples were taken at 8:00 am and 2:00 pm on October 25, 1957, at heights of approximately 1.5, 4.5, 7.0, and 10 ft above ground. Full sets of bud samples were taken from the southwest and from the northeast sides of the tree. The samples were placed in weighing bottles in the field and taken immediately to the laboratory for moisture content determinations. Fresh and oven dry weights (48 hrs at 75°C and then placed in a desiccator for 30 min) were obtained and moisture contents expressed on a dry weight basis. Weighing was done on an analytical balance.

During the experiment environmental conditions were conducive to high transpiration. The day was bright and clear

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with 8 hrs of bright sunshine, a maximum temperature of 54°F, a minimum temperature of 34°F, and a mean temperature of 46.0°F. The mean relative humidity was 65.7 percent, which was the lowest average relative humidity recorded for several days. On the preceding day 0.37 in of rain fell over an 8-hr period.

Another experiment was performed to investigate the amount of variation in moisture contents of buds during various times of the day. During the late afternoon of September 26, 1957, a number of branches of an American elm tree, 16 inches d.b.h., in full leaf, were tagged and numbered. All the tagged branches were on the southwest side of the tree between the 5- and 8-foot level. All buds on approximately half of the tagged branches were carefully coated with mineral oil with a small brush in an effort to prevent transpirational loss from buds. The following morning at 8:00 am samples consisting of 15 lateral buds each were taken from a branch with coated buds and also from a branch with uncoated buds. Additional samples of coated and uncoated buds were taken at 2-hr intervals until midnight. Moisture contents of all samples were determined as previously described.

The day of the experiment turned out to be clear with 9.1 hrs of bright sunshine recorded. Temperatures ranged from 57° to 29°F with an average temperature of 43.0°F. The mean relative humidity was 41.0 percent. This was the lowest mean relative humidity recorded during the whole month of September. No precipitation was recorded for four days prior to the experiment.

Another experiment was performed on diurnal variations in moisture contents of buds under conditions which did not favor high transpiration rates. The observations were taken on November 10, 1957. The temperature range was from 39° to 29°F, with a mean of 34°F and a mean relative humidity of 54.1 percent. The day was clear until 10:00 am and intermittently cloudy thereafter. Only 6.1 hrs of bright sunshine were recorded. Moisture contents of terminal and lateral buds of a Scotch pine (*Pinus sylvestris* L.) tree that was 8 ft 10 in high were determined at 8:00 am and 2:00 pm. Samples of 15 buds each were taken at approximately 0.5, 1.5, 2.5, 4.0, 5.5, and 7.0 ft above ground. Full sets of samples were taken from the southwest and northeast sides of the tree.

Excised buds. Transpirational losses of excised buds of American elm and white pine were determined for several days by a modification of a method described by Burstrom (1948). The following procedure was performed for each species. One hundred buds were cut off with a razor blade at the point of attachment, then mixed and divided into two groups of 50 buds each. One group of 50 buds was placed in a tared weighing bottle for moisture content determination. The other 50 buds were placed in an upright position in an open petri dish containing a mixture of approximately equal portions of vaseline and paraffin. The bases of the buds were rapidly fixed in this mixture and the petri dishes were then placed in an open-sided shelter on the roof of a building in order to expose the buds to the out-of-doors. The buds were not exposed to direct sunlight. Each day thereafter, at 8:00 am and 2:00 pm the dishes were brought to the laboratory and weighed on an analytical balance. Loss in weight was assumed to represent transpirational loss.

Results and Discussion

The moisture contents of attached white pine buds were much higher at 8:00 am than at 2:00 pm at all heights sampled (Table 1). The influence of sampling time was significant at the 1 percent level but effects of heights from which samples were taken and effects of exposure were not significant.

Diurnal variations in moisture contents of attached American elm buds are shown in Figure 1. Moisture contents of both coated and uncoated buds decreased during the morning hours, remained at low

levels during the afternoon, and then increased during the early evening hours beginning sometime after 6:00 pm. The effect of time of day was significant at the 5 percent level, but not at the 1 percent level. The effect of coating the buds was significant at the 1 percent level.

The 8:00 am moisture content of attached Scotch pine buds averaged 91.4 percent while the 2:00 pm values averaged 89.4 percent. These differences were not statistically significant. In addition no significant differences were found due to exposure or height of sampling. The moisture contents of Scotch pine buds were much lower than those of white pine or American elm.

Daily transpiration rates of excised American elm and white pine buds from November 8 to November 19, 1957, are given in Figure 2. Weather conditions for the same period are summarized in Table 2. The amount of transpirational loss per bud was much greater in elm than in pine. The elm buds had more fresh weight and more exposed surface per bud. In both species transpiration rates varied greatly on different days. Transpiration decreased steadily from November 9 to November 13. The rate increased rapidly after this date, and

TABLE 1. Moisture contents (percent O.D. wt.) of white pine buds at 8:00 am and 2:00 pm at various heights and two exposures. Data for October 25, 1957.

	Height above ground (feet)			
Exposure	1.5	4.5	7.0	10.0
		8:00 am		
Southwest	149.2	147.3	159.2	142.6
Northeast	145.4	148.9	149.2	147.5
Mean	147.3	148.1	154.2	145.1
		2:00 pm		
Southwest	121.1	114.5	119.4	115.8
Northeast	132.9	118.2	114.6	119.7
Mean	127.0	116.4	117.0	117.8

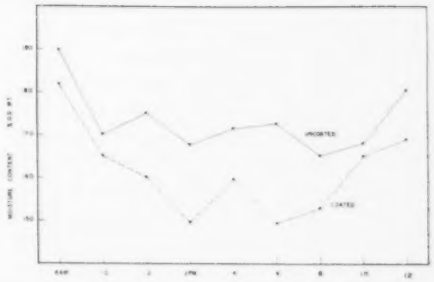

FIGURE 1. *Moisture contents of attached buds of American elm at various times of the day. Upper curve is for uncoated buds. Lower curve is for buds coated with mineral oil. Data for September 27, 1957.*

decreased again beginning on November 17.

Variations in amounts of water lost by transpiration (or gained by absorption from the air) between 8:00 am and 2:00 pm for several days are given on a dry weight basis for excised American elm and white pine buds in Figure 3. Again the rate of water loss or gain was variable. Water loss on a dry weight basis was greater for elm than for pine buds. On November 8 white pine buds absorbed a significant amount of water from the air, and they absorbed a small amount on November 13. In contrast elm buds always showed a net water loss. The pattern of transpirational loss during the 8:00 am to 2:00 pm interval was similar for both species. On days when it was high for one species it generally was high for the other also.

Under conditions favoring high transpiration rates large diurnal variations occurred in moisture contents of dormant buds on trees in full leaf. When atmospheric conditions did not favor high transpiration rates diurnal fluctuations in moisture contents of buds were low.

Whereas bud scales greatly impede loss of moisture from buds they do not completely prevent transpirational loss (Wiegand, 1906; Burstrom and Krogh, 1947; Burstrom, 1948). Burstrom (1948)

found that the rate of bud transpiration per unit of surface did not differ greatly from the rate of cuticular transpiration of leaves. Burstrom also concluded that transpiration of excised buds under standard humidity and temperature conditions was proportional to the water deficit of the air and water content of the buds. However, the present study shows that under normal environmental fluctuations transpirational loss of buds was controlled largely by changes in the evaporating power of the atmosphere (Fig. 2, Table 2). It should be pointed out, however, that the initial moisture contents of the buds used in the present experiment were high. Over a 10-day period the rate of transpiration changed rapidly as the evaporativity of the air changed despite the fact that the buds were continually becoming drier.

Although transpiration of excised buds varied greatly it was as high at the end as it was at the beginning of an experiment extending over several days (Fig. 3). These changes in rate of transpiration were correlated with changes in vapor pressure gradients.

Some of the decrease in moisture contents of attached buds during the day may

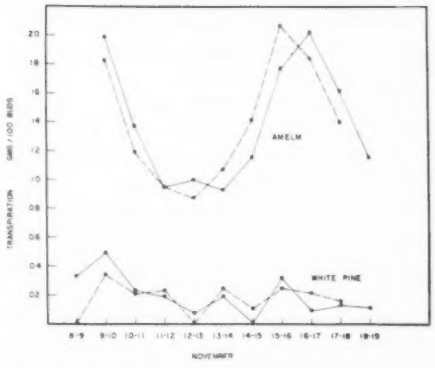

FIGURE 2. *Daily transpiration of excised buds of American elm and eastern white pine for the period from November 8 to November 19, 1957. Solid lines represent 24-hr transpiration from 8:00 am to 8:00 am. Dashed lines represent 24-hr transpiration from 2:00 pm to 2:00 pm.*

be attributable to translocation of water from buds to other parts of the tree. This view is supported by the observation that a decrease in moisture content during the day and an increase at night occurred in buds which were coated with mineral oil and which presumably had their transpira-

TABLE 2. Weather Summary for November 8-19, 1957, Amherst, Mass.

Date (Nov.)	Temperature Max.	Min.	Mean	Mean relative humidity	Bright sun	Precipitation Time	Amount
	Degrees F			*Percent*	*Hours*		*Inches*
8	62	28	45	83.3	1.0	7-12 pm	0.40
9	50	33	41.5	56.0	5.9	0-1 am	0.17
10	39	29	34.0	54.7	6.1	---	---
11	41	20	30.5	51.3	7.3	---	---
12	54	22	38.0	56.0	7.0	---	---
13	55	24	39.5	69.0	6.5	---	---
14	60	41	50.5	80.3	1.6	9-12 pm	0.18
15	65	43	54.0	74.0	5.5	0-7 am	0.55
16	59	32	45.5	83.7	6.0	---	---
17	56	41	48.5	75.3	4.0	---	---
18	52	39	45.5	78.3	6.0	9-12 pm	0.56
19	65	42	53.5	95.3	0.0	0 am-9 pm	0.95

tion eliminated or greatly impeded. In fact, diurnal variations in moisture contents of coated buds were greater than of uncoated buds. Possibly the reduction of transpiration pull in coated buds rendered them more susceptible to water depletion by the high diffusion pressure deficits which develop in leaves during the day when absorption through the roots lags behind foliar transpiration.

Occasionally buds absorb moisture from the air. Such absorption was not evident when changes in moisture contents of excised buds were computed over a 24-hr period (Fig. 2), but its occasional occurrence was apparent when moisture content changes were calculated over a shorter time interval (Fig. 3). Burstrom (1948) found that under controlled conditions bud transpiration took place three times faster than absorption when they were compared at equally large but oppositely directed vapor pressure differences. Burstrom concluded that absorption of water by buds had no real ecological significance even under the most favorable conditions for absorption.

When soil moisture supplies are low and the evaporativity of the air is high very large diurnal fluctuations may occur in moisture contents of buds. For example, on October 3, 1957, following a period of drought a sample of 100 American elm buds taken at 8:00 am had a moisture content of 176.5 percent while a sample of 100 buds taken at 2:00 pm of the same day had a moisture content of only 74.14 percent (oven dry weight basis).

These experiments do not suggest that the large fluctuations in moisture contents of buds that were observed occur in all species or on all days. Such variations undoubtedly are influenced by many factors including soil moisture conditions, moisture contents of buds at the beginning of the day, species, size and shape of buds, maturity of buds, and vapor pressure gradients.

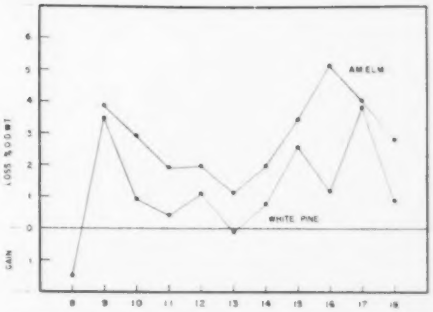

FIGURE 3. *Water loss by transpiration or gain by absorption of excised buds of American elm and eastern white pine for 6-hr periods (8:00 am to 2:00 pm) on consecutive days from November 8 to November 18, 1957.*

Summary

1. Under conditions conducive to high transpiration diurnal variations occurred in moisture contents of dormant buds on trees in full leaf. Moisture contents of dormant buds decreased during the morning, remained low during the afternoon, and increased during the evening hours.

2. Diurnal variations in moisture contents of dormant buds were attributed to bud transpiration, internal redistribution of moisture within the tree, and absorption of moisture from the atmosphere.

3. Transpiration of excised buds varied greatly on different days and was influenced more by changes in weather conditions than by moisture contents of buds.

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Recreational Use of Wild Lands

By C. Frank Brockman. McGraw-Hill Book Company, Inc., New York. 346 pp. $8.50.

Review by Grant W. Sharpe
The University of Michigan, Ann Arbor

Public recreation on public lands got its beginning in the United States, and has grown steadily in scope and importance. Suddenly the existing public land, set up originally for recreation is overcrowded. The vacationist, with his surplus of time, money, and variety of transportation media, is spilling into the managed public and private forest. Catering to tourists is more than providing motels and service stations, as any forester with the National Park Service or Forest Service will tell you. The forester becomes involved, whether he wants to be or not, for the forest he manages carries its own invitation to the ubiquitous tourist.

When most foresters took their professional training, usually only those who planned to specialize in recreation concerned themselves with such an "impractical" course as forest recreation. Even today, with recreation complicating the work of foresters, few *if any* forestry schools require of its graduates a course in forest recreation. Any forester directly concerned with recreation, or merely alarmed at this invasion of his territory will find in Frank Brockman's book a comprehensive study of the outdoor recreational field.

The book begins with the importance of wild land recreation, its needs, responsibilities, and objectives, in modern life. Following this is the section on the historical development of recreation in relation to the conservation movement in the United States. Next, the types of public and private agencies administering recreation lands and how each fits into the national recreation picture are discussed.

The chapter on the economic value of recreation lands in which the difficulties, dangers, and advantages of economically evaluating such lands are emphasized, is especially pertinent at this time.

The forward looking forester would be well advised to inform himself on the various aspects of planning, development, and administration of recreational land management. Prof. Brockman's book, on the basis of his many years experience in this field, will prove ideal as this informational source for both the graduate forester and the student.

Hardwood Reproduction in the River Bottoms of Southern Illinois

BY
JOHN F. HOSNER
L. S. MINCKLER

THE BROAD GROUP of forest types referred to as bottomland hardwoods occur along the major streams in the eastern United States. In Illinois, they occupy one-fifth of all commercial forest land (King and Winters, 1952). These forests are important because they are composed primarily of valuable timber species capable of making extremely rapid growth on the better bottomland sites.

As an aid to understanding how to reproduce bottomland hardwoods a field study was conducted (1) to determine the status of tree reproduction in bottomlands and (2) to relate the reproduction of species and species groups to certain stand and site factors.

Reproduction was evaluated according to broad forest types, density of overstory, size of canopy openings, density of ground vegetational cover, depth of litter, and the available water-holding capacity of the surface soil and subsoil.

Procedures

Field sampling. The field procedure consisted of locating 62 sample stands in several different bottomland types followed by a systematic sampling to determine the abundance of regeneration of different species. The tree species studied and discussed here are: green ash (*Fraxinus pennsylvanica* Marsh.); boxelder (*Acer negundo* L.); eastern cottonwood (*Populus deltoides* Bartr.); American elm (*Ulmus americana* L.); hackberry (*Celtis occidentalis* L. and *Celtis laevigata* Willd.); hickory and pecan (*Carya spp.*); red maple (*Acer rubrum* L.); silver maple (*Acer saccharinum* L.); oaks (*Quercus lyrata* Walt., *Quercus palustris* Muenchh., *Quercus falcata* var. *pagodaefolia* Ell., *Quercus macrocarpa* Michx., *Quercus shumardii* Buckl., *Quercus michauxii.* Nutt.); sweetgum (*Liquidambar styraciflua* L.); sycamore (*Platanus occidentalis* L.); willow (*Salix interior* Rowlee and *Salix nigra* Marsh.).

Criteria used for selecting bottomland areas were as follows:

1. If forested, the site had to be stocked with hardwoods of natural origin and subject to periodic overflow.
2. Each sample area had to be at least three acres in size.
3. Each area had to be confined to one topographic site as described by Putnam (1951). The sites included in the study were all on first bottoms which are subject to flooding at any out-of-bank stage of the stream unless protected by levees. The first bottom sites included ridges, flats, sloughs, and river fronts. No terrace sites were included. The ridges are the highest ground,

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commonly ranging from 2 to 15 feet above adjoining flats. The flats constitute the general terrain between ridges. Sloughs are shallow depressions in which water collects but normally disappears during the first half of the growing season. Fronts are new land deposits along stream margins.

4. Each area had to be free of fires, cutting, or grazing for at least 5 years prior to sampling. It was necessary to use some areas lightly cut or burned, but all areas were excluded where cutting or fire appeared to have affected the composition and amount of reproduction.

The following information was taken on each area selected for sampling:

1. Basal area per acre by species was obtained by systematically selecting 12 points on each forested area and using the plotless timber cruising technique as explained by Grosenbaugh (1952).

2. The soil was sampled by taking a separate composite sample of the surface soil (0-6 inch depth) and the subsoil (24-30 inch depth). The soil from four systematically located spots on each area made up each composite sample.

In addition to the above information, reproduction was sampled systematically by locating 50 milacre plots on each 3-acre area and recording the reproduction by age classes and species. The age classes used were 0 to 2 years old, 3 to 5 years old, and over 5 years old but less than 4.5 inches d.b.h. Ages were determined from terminal bud scars and ring counts. As each milacre plot was taken, the following associated environmental conditions were recorded: (1) depth of litter in inches, (2) size of canopy opening, if any, over each milacre plot, and (3) the precent of each milacre plot covered with ground vegetation below the shrub layer.

Soil analysis. Moisture equivalent and approximations of wilting percentages were determined from soil samples that had previously been air dried and reduced to a maximum particle size of two mm. Moisture equivalents were determined by subjecting the soil fractions to a centrifugal force of 1,000 times gravity in a soil centrifuge and determining the water content as a percentage of oven-dry weight (Briggs and McLane, 1907).

An approximation of the wilting percentage was determined by subjecting the soil sample to 15 atmospheres of pressure in a pressure membrane apparatus according to a procedure described by Richards (1947). The difference between moisture equivalent and wilting percentage was assumed to be the capacity of the soil for holding available water.

Analysis of reproduction data. The analysis of reproduction was made by determining the quantity by species and species groups. This was related to stand and site factors assumed to be important. Based upon the quantities of reproduction, and its relation to the associated factors, a subjective evaluation of the significance of the data was made. Because of the variation in the limited number of samples, a single factor analysis was made. Any confounding of data, as a result of the single factor analysis, which appears to alter results, is noted in the text. Only gross differences or consistent trends were considered worthy of note.

Results

Seedling density by broad site-types. For the purpose of comparing stocking by types all areas were grouped into 5 categories of site or vegetation—(1) newly formed land with seedling and sapling reproduction, (2) old fields with seedling and sapling reproduction, (3) cottonwood-willow, (4) mixed soft-hardwoods, and (5) mixed hard-hardwoods. The last three follow the classification of the Illinois Technical Forestry Association (1947). Areas of newly formed land consisted of recent alluvial deposits of soil in the form of sandbars or thick coverings on former low spots. The old fields were areas that had been cleared for agriculture and later abandoned. No areas with trees larger than 4.5 inches d.b.h. were classified in the latter two types.

The cottonwood-willow, mixed soft-hardwoods and the mixed hard-hardwoods were identified by the species making up at least 50 percent of the basal area in dominant and codominant trees. The basal area of cottonwood-willow stands consisted of 50 percent or more of these two species. The basal area of mixed soft-hardwood stands consisted of 50 percent or more silver maple, green ash, sweetgum, sycamore, hackberry, American elm and a few other hardwoods. The mixed hard-hardwood stands were dominated by hickories and oaks but also contained some ash, elm and hackberry and miscellaneous species.

Major tree species are grouped for comparative purposes (Table 1). Except for the miscellaneous groups, species within groups are generally similar in seeding habits, tolerance, and other gross silvicultural characteristics. Deciduous holly (*Ilex decidua* Walt.), buttonbush (*Cephalanthus occidentalis* L.), and swamp-privet (*Forestiera acuminata* Michx.) make up the largest segment of the miscellaneous group although this group also included small numbers of persimmon (*Diospyros virginia* L.), winged elm (*Ulmus alata* Michx.), swamp cottonwood (*Populus heterophylla* L.), red maple (*Acer rubrum* L.) and a few other minor species.

Reproduction was plentiful on all areas but the differences in quantity among species were often quite distinct (Table 1). Newly formed land had by far the largest number of seedlings and old fields were second. The cottonwood-willow type had the fewest seedlings. On old fields the elm-hackberry-boxelder and the cottonwood-willow species groups of tree reproduction predominated. In the former group the elms outnumbered by approximately 10 times the boxelder and hackberry combined. The ash-silver maple group also occurred in important numbers on old fields but seedlings of other species were scarce.

On newly-formed land cottonwood and willow seedlings outnumbered all other species taken together. Approximately 80 percent of the elm-hackberry-boxelder seedlings in this type were boxelder. They were usually a few years younger than the cottonwood-willow seedlings. In the cottonwood-willow type, ash-silver maple and elm-hackberry-boxelder were found in approximately equal numbers and both groups

TABLE 1. Seedlings per acre by species groups for five broad categories of forest site-types.

Old fields		Newly formed land		Cottonwood-willow type		Mixed soft-hardwood type		Mixed hard-hardwood type	
Species groups	Seedlings	Species groups	Seedlings	Species groups	Seedlings	Species groups	Seedlings	Species groups	Seedlings
	No.		*No.*		*No.*		*No.*		*No.*
Elm-hackberry boxelder	1823	Cottonwood-willow	6986	Elm-hackberry-boxelder	592	Elm-hackberry-boxelder	1484	Elm-hackberry-boxelder	821
Cottonwood-willow	1760	Elm-hackberry-boxelder	480	Silver maple-ash	576	Silver maple-ash	1015	Silver maple-ash	672
Silver maple-ash	562	Sycamore-sweetgum	270	Sycamore-sweetgum	13	Sycamore-sweetgum	50	Oaks	541
Sycamore-sweetgum	106	Silver maple-ash	6	Hickory-pecan	12	Hickory-pecan	40	Hickory-pecan	207
Oaks	23	Oaks	0	Oaks	4	Cottonwood-willow	27	Sycamore-sweetgum	42
Hickory-pecan	20	Hickory-pecan	0	Cottonwood-willow	90	Oaks	109	Cottonwood-willow	16
Miscellaneous	149	Miscellaneous	45	Miscellaneous	238	Miscellaneous	385	Miscellaneous	270
Totals	4443		7787		1534		3110		2569

were represented by more than twice as much reproduction as any of the other groups. Except for the miscellaneous species, no other group had more than about 100 seedlings per acre.

The mixed soft-hardwood type had about twice as many seedlings as the cottonwood-willow type. The major portion of reproduction in the mixed hard-hardwood type consisted of elm-hackberry-boxelder, silver maple-ash, and the oaks. The oaks, mostly pin oak (*Quercus palustris*) hickory, and pecan (*Carya illinoensis*) were more abundant in this type than in any other. Less than 60 seedlings per acre of cottonwood, willow, sycamore, and sweetgum were found in the mixed hard-hardwood type.

Seedling density associated with basal area of the overstory. The basal area of the plots sampled varied from 38 to 120 sq ft per acre. Most of this variation could be attributed to differences in intensities of past cutting; some was probably the result of species composition and site.

With the exception of cottonwood-willow, there was no strong relationship between the density of seedlings 1 to 5 years old and the basal area of the overstory (Table 2). Seedlings of these two very intolerant species, however, increased with a decrease in the overstory. Cottonwood and willow do not survive even under a moderately dense canopy. In addition, several species tended toward low seedling density under a sparse overstory—a fact probably related to the presence of a denser ground cover.

The older seedlings of silver maple, apparently established before the development of a heavy ground cover, were much more abundant in sparse than in dense stands (Table 3). Heavy overhead shade, on the other hand, resulted in reduced numbers of this intolerant species. Some, of course, will persist in small openings even in stands with an overall basal area of 100 sq ft or more. The same trend is shown by pin oak. Pin oak seedlings will live for 2 to 3 years under dense canopies but die soon thereafter (Minckler, 1957). Early seedling mortality undoubtedly occurs with the other intolerant species such as cottonwood, willow (Maisenhelder and Heavin, 1956), and sycamore (Merz, 1958), but the present data are insufficient to show this.

TABLE 2. Seedlings[1] per acre, age one to five years, by species groups and basal area of overstory.

Species group	Basal area of overstory (sq ft per acre)			
	38-50	51-75	76-100	Over 100
	Number of seedlings per acre			
Silver maple-ash	984	604	576	926
Hackberry-boxelder	393	221	603	396
Elm	265	687	695	382
Cottonwood-willow	155	6	30	4
Oaks[2]	62	125	403	134
Hickory-pecan	58	193	74	38
Sycamore-sweetgum	33	82	17	24
Milscellaneous	229	319	230	576
Totals	2175	2237	2638	2480

[1]Based on the 51 sample areas which had an overstory. Includes all plots of cottonwood-willow, mixed soft-hardwoods and mixed hard-hardwoods.

[2]Approximately 90 percent pin oak.

TABLE 3. Seedlings by species, age class, and basal area of overstory.

Species	Age class	Basal area of overstory (sq ft per acre) 38-50	51-75	76-100	Over 100
	Years	*Mean number of seedlings per acre*			
Silver maple	1-2	129	122	200	386
	3-5	429	182	149	216
	Over 5	133	95	40	34
Pin oak	1-2	16	28	97	110
	3-5	33	62	285	10
	Over 5	56	23	24	0

Reproduction associated with size of canopy openings. The degree of overhead cover was recorded for each milacre plot and the opening sizes were expressed in relation to the height of the surrounding dominant trees. In general, young seedlings 1 and 2 years of age were more abundant under canopies than in the openings (Table 4). This was true of all species groups except sycamore-sweetgum and cottonwood-willow. On the other hand, seedlings aged 3 to 5 years showed the opposite trend, especially silver maple, cottonwood-willow, and boxelder-hackberry (Table 5).

All species except cottonwood, willow, sycamore and sweetgum have reproduced adequately under the heavier canopy conditions. But it was evident that a dense canopy becomes limiting as the seedlings grow older. The larger number of younger seedlings under the denser canopy is probably associated with the lower density of ground vegetation prevalent in the deep shade. Seed distribution for the heavier seeded species may also be a factor. As the canopy is opened up the increased light stimulates both herbaceous ground vegetation and tree seedlings. Appreciable numbers of seedlings do survive (Table 5).

With the possible exceptions of cottonwood and willow, the data indicate that openings are not needed for germination and early survival. However, after one

TABLE 4. Seedlings 1 to 2 years old by species and diameter of canopy openings, where h equals height of stand.

Species or species group	0	Diameter of openings in canopy $< \frac{1}{2}$ h	$\frac{1}{2}$ h - 1 h	$>$ 1 h
		Mean number of seedlings per acre		
Elm	384	493	358	205
Boxelder-hackberry	300	235	88	141
Silver maple	285	184	210	119
Oaks	149	57	61	19
Ash	94	183	120	61
Pecan-hickory	85	33	41	13
Sycamore-sweetgum	3	15	23	6
Cottonwood-willow	1	10	8	10
Miscellaenous	131	145	51	45
Totals	1432	1355	960	619

or two years apparently the seedlings of most species begin to die unless openings are made. Furthermore, rapid growth is achieved only in openings (Minckler, 1958), and lack of openings favors the less desirable and more tolerant species such as American elm, hackberry, and boxelder, as well as dogwood and shrubs.

Reproduction associated with ground cover conditions. Ground vegetation arbitrarily was grouped for comparative purposes into the following classes: (1) heavy—70 percent of the soil surface shaded by lower vegetation, (2) medium—less than 70 percent but not less than 30 percent of the soil surface shaded by lower vegetation, and (3) light—30 percent or less of the soil shaded by lower vegetation.

Only reproduction in the youngest age class, 0-2 years, is reported because such seedlings are affected most by the ground vegetation present (Table 6).

Ground cover varied from annual grasses and sedges less than 1 foot in length to perennial herbs and vines 3 to 4 feet in height. Most of this variation was associated with different amounts of overhead canopy cover and with differences in surface drainage. However, the thin canopies of cottonwood and willow stands did not seem to inhibit the lower vegetation. Cottonwood and willow areas were uniformly covered with heavy ground vegetation except where subjected to standing water for several weeks or more during the growing season.

TABLE 6. Seedlings one and two years old by species groups and ground cover conditions.

Species group	Ground Cover		
	Light	Medium	Heavy
	Mean number per acre		
Cottonwood-willow	546	1	20
Elm-hackberry-boxelder	328	1036	533
Silver maple-ash	272	369	215
Miscellaneous	176	153	28
Oaks	91	101	23
Pecan-hickories	66	51	12
Totals	1479	1711	831

The most common ground cover in the cottonwood-willow type consisted of woody vines, particularly pepper vine (*Ampelopsis arborea* L.), grapevines (*Vitis spp.*), Virginia creeper (*Parthenocissus quinquefolia* L., Planch.), dewberry (*Rubus* spp.), trumpet creeper (*Campsis radicans* L.), and poison ivy (*Toxicodendron radicans* L. Kuntze). Except for pepper vine, most of these same species were found in the more open stands of mixed soft-hardwoods and mixed hard-

TABLE 5. Seedlings 3 to 5 years old by species and diameter of canopy openings, where h equals height of stand.

Species or species group	Diameter of openings in canopy			
	0	< ½ h	½ h to 1 h	> 1 h
		Mean number per acre		
Elm	134	224	213	240
Boxelder-hackberry	120	232	313	471
Silver maple	39	213	393	619
Oaks	153	146	103	189
Ash	89	273	253	163
Pecan-hickory	44	36	40	68
Sycamore-sweetgum	10	45	25	32
Cottonwood-willow	8	20	68	157
Miscellaneous	172	199	169	308
Totals	769	1388	1577	2247

hardwoods. Under the more closed canopies of these types, however, poison ivy and aster (*Aster* spp.) were the chief species present. Areas with poor surface drainage were often covered with lizard's tail (*Saururus cenuus* L.), jewel weed (*Impatiens pallida* Nutt.) and sedges. One-seeded bur cucumber (*Cicyos angulatus* L.), and pepper vine often formed complete mats of vegetation in more open stands of cottonwood-willow and mixed soft-hardwood stands or on shaded areas. Among the species making up the lower vegetation, cucumber vine, pepper-vine, trumpet creeper, and grape vines seem to offer most competition to tree seedlings.

Cottonwood and willow seedlings were found in appreciable numbers only on areas with light ground cover. American elm, hackberry, and boxelder were much less sensitive to the increasing competition and were found abundantly on areas with both medium and heavy competition. Elm-hackberry-boxelder were by far the most common species of young seedlings on areas with heavy cover. Young maple-ash seedlings occurred in all cover types but tended to be scarce in heavy vegetation. The miscellaneous species, the oaks, and the pecan-hickories were infrequent on areas with ground cover.

The species of plants making up the ground cover vegetation vary from area to area and may be just as important as the amount. Secondly, the ground cover varies with the time observed during the growing season. For example, cucumber vine is hardly noticeable in early summer, but often presents a tangled mass of almost impenetrable vegetation in late summer. Thirdly, the amount of ground cover varies directly with overhead light conditions—the more sunlight reaching the forest floor, the more growth of vegetation. Lastly, ground cover is also affected by moisture. An abundance of moisture which would ordinarily be expected to be beneficial to seedling survival is also conducive to excessive growth of lower vegetation, offering increased competition. Only low spots that impound water during the early part of the growing season are free of heavy ground cover. In general, the data shown in Table 5 substantiate earlier statements that openings in cut stands are soon covered with a heavy growth of lower vegetation that may retard subsequent regeneration of tree seedlings. Unless the seedlings are established before cutting or concurrently with the ground vegetation, regeneration of desirable species is usually reduced.

Reproduction associated with different litter depths. Litter consisted mostly of tree leaves, although the remains of other vegetation were apparent on some areas. Leaves of cottonwood, willow, silver maple, and boxelder disintegrate quite rapidly and form a different type of litter than leaves of red oaks which disintegrate more slowly and form a tougher and more matted litter. Thus, there were variations in litter according to species in the stand.

Large variations in litter depth were also caused by water movement. Swift moving water of earlier floods often left the ground bare. In some cases, however, the areas act as settling basins and thick layers of litter are accumulated.

Litter sampling was done throughout the late spring and the summer months. However, differences due to season were not readily noticeable and were not considered important. Litter depths were grouped into 3 classes for the purpose of showing relations with the amount and kind of reproduction (Table 7). Only the seedlings 2 years and under were used in comparing the effects of litter depths because: (a) except for a slight mulching effect litter could hardly be expected to have much influence on seedlings more than 2 years old, and (b) litter conditions are apt to change rapidly with time.

Reproduction of all species declined with heavier litter (Table 7). Of the plots with over 2 inches of litter 47 percent did not have a single young seedling of any species as compared to 20 percent in the ½- to 2-inch litter depth class. The largest number

TABLE 7. Seedlings one and two years old by species groups and depth of litter (in inches).

Species group	Light over ½ in	Medium ½ - 2 in	Heavy over 2 in
	Mean number per acre		
Elm	326	619	271
Cottonwood	151	0	0
Willow-sycamore	305	0	0
Boxelder	121	90	35
Ash	117	55	0
Silver maple	106	506	24
Hackberry	68	180	94
Oaks	49	174	35
Hickory	43	54	0
Miscellaneous	313	208	12

of seedlings of American elm, silver maple, hackberry and the oaks were found on areas with ½ inch to 2 inches of litter. The miscellaneous species, eastern cottonwood, willow, sycamore, and ash were found in greatest numbers on areas with a light litter. Eastern cottonwood, willow, sycamore, ash, pecan, and hickory were totally absent on areas with over 2 inches of litter. Willow, sycamore, and cottonwood were also absent on areas with medium litter. Heavy litter apparently had the least retarding effect on elm, hackberry, and the oaks.

Reproduction associated with the capacity of the surface soil to hold available water. The reproduction of cottonwood-willow was most abundant on the lighter-textured surface soils and absent on those of heaviest texture (Table 8). The relation between abundance of cottonwood-willow reproduction and available water holding capacity was very strong. A contributing factor seemed to be the lack of competition on the lighter soils. Greenhouse tests indicated that, where moisture is not limiting, germination and early establishment of cottonwood is equally good on clay soils with high available moisture constants as on sandy soils with low available moisture constants.[3] Reproduction of the elm-hackberry-boxelder group occurred abundantly on all soils except the lightest. Boxelder seedlings were the major component on the soils of 13 to 16 percent moisture capacity whereas elm made up the largest part in the soils of 21 to 25 percent. Silver maple-ash were also well represented on all soils except those of lowest moisture capacity (Table 8). Reproduction of the hickory-pecan, oaks, and miscellaneous species tended to increaese with an increase in moisture holding capacity of the surface soil.

[3]J. F. Hosner (unpublished data), 1958.

TABLE 8. Mean numbers of seedlings per acre by species associated with available water holding capacity in the surface soil (0-6 inch depth).

Species group	Number of seedlings when percent of available soil moisture capacity is— 8-12	13-16	17-20	21-25
		Number		
Cottonwood-willow	5140	920	25	0
Elm-hackberry-boxelder	170	1866	870	1220
Silver maple-ash	89	671	678	685
Sycamore-sweetgum	115	124	31	50
Oaks	0	64	277	45
Hickory-pecan	0	77	90	110
Miscellaneous	9	186	314	360
Totals	5523	3908	2285	2470

Reproduction associated with the capacity of the subsoil to hold available water. The available soil moisture of the subsoil was the difference between moisture equivalent and wilting percentage for the 24- to 30-inch zone of the soil. The relation between water holding capacity and number of seedlings is evaluated by species (Table 9).

Cottonwood-willow reproduction was associated strongly with low available water of the subsoil. These soils were mostly found on the newly formed land. In the 8 to 12 percentage group cottonwood and willow seedlings were more than 6 times as numerous than all other species combined. Cottonwood-willow were scarce where the the available moisture holding capacity was highest.

Reproduction of the elm-hackberry-boxelder group was consistently high on all soils, ranking either first or second in all groups. Silver maple-ash also reproduced well except where moisture holding capacities were low.

It seems clear that the reproduction of some species groups is rather closely related to available moisture holding capacity of the subsoil. However, this may not be a direct cause and effect relationship. For example, it is likely that increased reproduction of the heavy-seeded species on the soils with higher clay content is due in part to the presence of a greater number of seed trees of these species (Hosner, 1957). Also, the lack of competition on the newly formed land with sandy soils seems to be a big factor in the establishment of cottonwood and willow. Cottonwood and willow seedlings cannot stand competition even from annual weeds and grasses (Barclay, 1924; Switzer, 1948; Putnam, 1951; Ware, 1955).

Discussion and Conclusion

Foresters, in referring to bottomland hardwoods, sometimes give the erroneous impression that bottomlands constitute a homogeneous and definitive set of conditions. However, as Putnam (1951) pointed out, there are 8 different major forest types with many variations, found on the bottomlands of the lower Mississippi river alone. These types together with the different soils, degrees of flooding, and topography present an extremely heterogeneous picture of forest conditions. Thus, there are many interacting variables affecting regeneration. It was beyond the scope of this survey to establish in detail the effects of the many variables on regeneration, but the present study does point out some of the salient factors pertaining to natural regeneration of bottomland hardwoods. These facts can be used as the basis for more definitive studies in the future.

In general, this study showed that an

TABLE 9. Mean number of seedlings per acre by species associated with available water holding capacity in the subsoil (24-30 inch depth).

Species group	Number of seedlings when percent of available soil moisture capacity is— 8-12	13-16	17-20	21-25
	Number			
Cottonwood-willow	6430	589	26	18
Elm-hackberry-boxelder	395	1495	762	839
Silver maple-ash	105	764	779	305
Sycamore-sweetgum	105	66	39	85
Oaks	0	147	244	269
Hickory-pecan	0	64	65	226
Miscellaneous	105	178	378	363
Totals	7140	3303	2293	2105

adequate number of seedlings of desirable forest trees occurs initially on all the bottomland sites studied, although the proportion varies by species from area to area. Except for newly formed land, where cottonwood predominates, undesirable species such as American elm, boxelder, and shrubby species such as privet, deciduous holly, and dogwood exceed the numbers of more desirable species. This does not mean, however, that the resulting stands will necessarily be predominantly composed of these poor species. Often, the better timber species tend to assert themselves by faster and more persistent growth.

Cottonwood and willow seedlings were associated with a rather specific set of environmental conditions. They were found in adequate numbers only on open areas exposed to direct sunlight for the greater part of the day, and nearly devoid of litter and ground cover. Thus, they were found to be reproducing satisfactorily only on newly formed land areas consisting of sandy soils with low moisture holding capacities, and on some old fields that had been subjected to heavy flooding. Reproduction of both these species in established stands was insignificant even where stocking was less than 50 sq ft of basal area per acre. No cottonwood and willow seedlings 0-2 years old were present on plots with either a heavy cover of ground vegetation or a litter depth of over ½ inch.

The other major species could not be as specifically associated with definite environmental conditions; however, certain trends were evident. Apparently, except for cottonwood and willow, other major bottomland species are able to germinate and become initially established under a wide range of soil and site conditions. But with most species, there was a tendency toward less reproduction where litter was deep, ground cover heavy, or overstories sparse. The latter two were related. Sparse overstories were accompanied by denser ground cover. Younger seedlings of pin oak and silver maple definitely increased under the heavier overstories, but the number of older seedlings dropped off sharply where the basal areas exceeded 100 sq ft per acre. Reproduction occurs under the closed canopy but tends to die out gradually unless the stand is opened. Openings are considered necessary to obtain adequate growth and to favor the better and usually more intolerant species (Minckler, 1958).

American elm, boxelder, silver maple, and green ash seedlings were the most abundant seedlings in all stands of timber. They were also strongly represented in the reproduction of old fields. Apparently these species are able to compete effectively over a wide range of conditions. There was more reproduction of elm than any other species on areas that had either a cover of heavy ground vegetation or a deep layer of litter.

Groupings according to available moisture constants of the 0 to 6 and 24 to 30 inch soil layers showed that cottonwood and willow reproduction was well represented only on sandy soils with a low moisture holding capacity. Conversely, hickory-pecan, oaks, and the miscellaneous species had definitely more reproduction on the heavier soils with high moisture holding capacities. However, it is not certain that moisture holding capacity, as such, is the chief factor involved. Another explanation is that the bare, open, sandy soils of the newly-formed land, where conditions were good for cottonwood-willow reproduction, generally had low water holding capacities. A contributing factor to the greater abundance of reproduction of heavy-seeded species on the heavier soils may be the more frequent occurrence of these species in the overstory and consequently a greater supply of seed.

In conclusion, American elm, boxelder, green ash, and silver maple were the most strongly represented timber species reproducing on bottomlands, except on newly formed land, where cottonwood and willow were the most numerous. Elm was by far the most ubiquitous bottomland species and was found in large numbers under the widest range of conditions.

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Death and Deterioration of Balsam Fir Weakened by Spruce Budworm Defoliation In Ontario

Part III. The Deterioration of Dead Trees

BY
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R. M. BELYEA

OUTBREAKS of the spruce budworm, *Choristoneura fumiferana* (Clem.), in eastern Canada have almost invariably resulted in widespread mortality of its host trees. In recent years in Ontario, large numbers of white spruce, *Picea glauca* (Moench) Voss, and black spruce, *Picea mariana* (Mill.) B.S.P., have died, and the immediate prospect is for the continuing destruction of these valuable species in the northwestern part of the province.[1]

These losses constitute an appreciable reduction in the commercial wood reserves of the province. After death, the trees remain suitable for utilization for a limited period only. In the past, forest operators have been reluctant to undertake large-scale salvage in areas of spruce budworm outbreak owing to the speed with which the trees die, and to a lack of knowledge concerning the progress of deterioration of the wood after death. This study was therefore carried out to determine, for a specific region, the identity and relative importance of the insects and fungi causing deterioration of balsam fir after death, and the rate at which that deterioration takes place. Since most of the balsam fir cut in that area is utilized in the manufacture of pulp, deterioration from the pulpwood point of view was emphasized in the study.

Between 1946 and 1951, comprehensive studies were undertaken on the complex of insect species attacking balsam fir weakened by spruce budworm defoliation, and the relationship between such attacks and tree death. These investigations were carried out in the region to the west and southwest of Lake Nipigon from the Black Sturgeon Lake Field Station, a field establishment of the Forest Insect Laboratory, Sault Ste. Marie, Ontario. Results of those studies have been reported in Parts I and II of this series (Belyea 1952a,b). The time of death and the associated history of insect infestation of several hundred balsam fir trees were recorded yearly during those studies. These trees, as well as a few that died before 1946 which were located in a

[1]Annual report of the Forest Insect and Disease Survey. Canada Department of Agriculture, Forest Biology Division, Science Service, 1957.

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permanent mortality plot established in 1943 by the Forest Insect Laboratory, provided the material upon which this report is based.

Method of Study

Early in the study it was realized that the appearance of dead trees was not a reliable indication of how long they had been dead, hence only those whose condition had been observed and recorded previously were studied. During the latter part of the field seasons of 1949 and 1950, 189 balsam fir trees for which accurate dates of death and history of associated insect attack were known, were selected for sectioning and examination. The trees were chosen to give a comparable sample for each yearly period since death, and, as far as possible, to give comparable representation of trees that died during winter and summer seasons.

The trees were cut as close to the ground as possible. Blocks 1 foot in length were then removed from the bole for entomological study at the base and at 8-foot intervals up to a 3-inch top. At each cut in the bole the d.i.b., diameter of heart rot, and the depth from the surface of any deterioration present were measured, and recorded on logarithmic tree measurement forms. Where necessary, logs were dissected to determine the extent of decays or deterioration which disappared in those logs. A description was recorded for each sap stain and sap rot, as was the causal organism if it could be readily recognized. Where rots could not be identified with certainty, cultures were made in the field from affected wood and sent to the Division of Botany and Plant Pathology, Department of Agriculture, Ottawa, for identification of the causal organisms.

Each 1-foot study block was barked, and the number of sawyer beetle entrance holes was recorded. The blocks were sectioned longitudinally to determine the depth to which deep-boring insect species had penetrated. Techniques used in studying the interrelationships between insects and fungi are described in detail later.

Compilation of Data

To assess progressive deterioration, it was necessary to classify the trees according to the length of time since death. From the records it was possible to assign a year of death to each tree. Those which died during the period from October to the following September were placed in the same death-year class. The relatively few trees on the permanent mortality plot were examined only once annually, but the remaining trees were examined each year at weekly or bi-weekly intervals from early May until late September from the time the plots were established in 1946 and 1947 until the trees died (Belyea 1952b). It was thus possible in the latter trees to designate the time of death as having occurred during either the summer months (May to September), or the winter months (October to April). These are logical periods from the point of view of associated insect attack, because the flight period of all of the species falls within the summer period (Belyea 1952a).

A further subdivision of the trees that died during the winter period was necessary, based on the history of attack by the sawyer beetle, *Monochamus scutellatus* Say. This insect, which is in flight from June to August, initially infests trees that died during the previous winter and during the current summer. However, during August it also attacks trees that do not die until the following winter, although not all trees dying during the winter are so infested. Since nearly all trees dying during the winter are attacked the following summer by the beetle, some trees eventually contain two populations of *M. scutellatus* larvae, one of which commenced its activity in the tree some 11 months before the other. Trees dying during the winter were therefore subdivided into two groups, depending on whether or not they had been attacked by *M. scutellatus* the previous summer.

For each 1-foot study block, the density of sawyer beetle entrance holes, that is, the number of holes per square foot of wood surface, was calculated.

The total merchantable volume of each tree in cubic feet, from stump height to a 3-inch top, was calculated from the area representing this volume on each tree measurement form. The volumes of heart rot, sap stain, and the different types of sap rot were determined in the same manner. Wood that retained its firmness when tested with the point of a sharp knife, and showed the presence of deteriorating agents only by a discoloration, was classed as sap stain or incipient deterioration. The average depth of radial penetration of visible deterioration for each tree was computed from the tree measurement forms.

Agents of Deterioration

Entomological. Belyea (1952a) has reported that of the 10 species of insects recorded as breeding in dying or newly dead balsam fir trees in the Lake Nipigon region, few cause actual damage to the wood of the tree. The bark beetle, *Pityokteines sparsus* Lec., the weevil, *Pissodes dubius* Rand., and the borer, *Tetropium cinnamopterum* Kby., do not penetrate the wood to any extent, their larval activity being confined almost exclusively to the inner bark and the wood surface.

A second group of species do penetrate the wood, but only to a limited degree. The ambrosia beetle, *Trypodendron lineatum* (Oliv.), *Serropalpus substriatus* Hald., and three siricids, *Sirex juvencus* (L.), *Sirex* sp. (*Noctilio* group), and *Urocerus albicornis* F., affect only the outer sapwood. In all of the trees sectioned, the greatest depth of penetration of any of these species was 1½ inches, with the bulk of the mines being 1 inch or less in depth and of relatively small diameter. They therefore affect a comparatively small volume of the wood, and cause no real damage from the practical point of view. While these insects do not damage the wood appreciably by their mining activity it will be shown that some of them may play a part in introducing deteriorating fungi into the sapwood of dead trees.

Only two insect species, both sawyer beetles, *Monochamus scutellatus* and *M. marmorator* Kby., mine deeply into the wood of dead balsam fir trees and possibly contribute directly to their deterioration. The mining habits of these two species are very similar, and it was not possible during this study to distinguish between their mines. However, *M. marmorator* was very scarce in the Lake Nipigon region during this study while *M. scutellatus* was very abundant, so that it could safely be assumed that the bulk of the borer damage encountered in dead trees was the work of *M. scutellatus*.

Mines of *M. scutellatus* penetrated to the center of the bole, regardless of diameter, of almost every tree sectioned two years or more after death. Thus, nearly all of the wood of dead balsam fir trees contained the u-shaped mines of this species, since the great majority of trees dying as a result of spruce budworm defoliation were heavily infested. In the manufacture of pulp the amount of wood fibre lost as a result of these mines may be significant,[2] although this possibility was not examined during this study. However, the deep penetration by the larvae does afford ready access to the inner wood for certain of the rot-inducing fungi.

Pathological. The deterioration of balsam firs that have died following spruce budworm outbreaks involves several of the sap-staining and sap-rotting groups of wood-destroying fungi. These fungi attack only dead trees, and are so named because they initiate infection from the outer sapwood. They are primarily responsible for the rapid deterioration of dead trees, gaining admission to the outer bole on insects or through the many avenues of entrance present in dead bark. Once dead, the sapwood, hitherto capable of resisting the invasion of harmful fungi, becomes exceedingly susceptible to attacks by these organisms, which then spread very rapidly and soon occupy most

[2]McNeel, W. Insects in jack pine pulpwood and their relationship with fungi. Ph.D. thesis, University of Wisconsin, 1955.

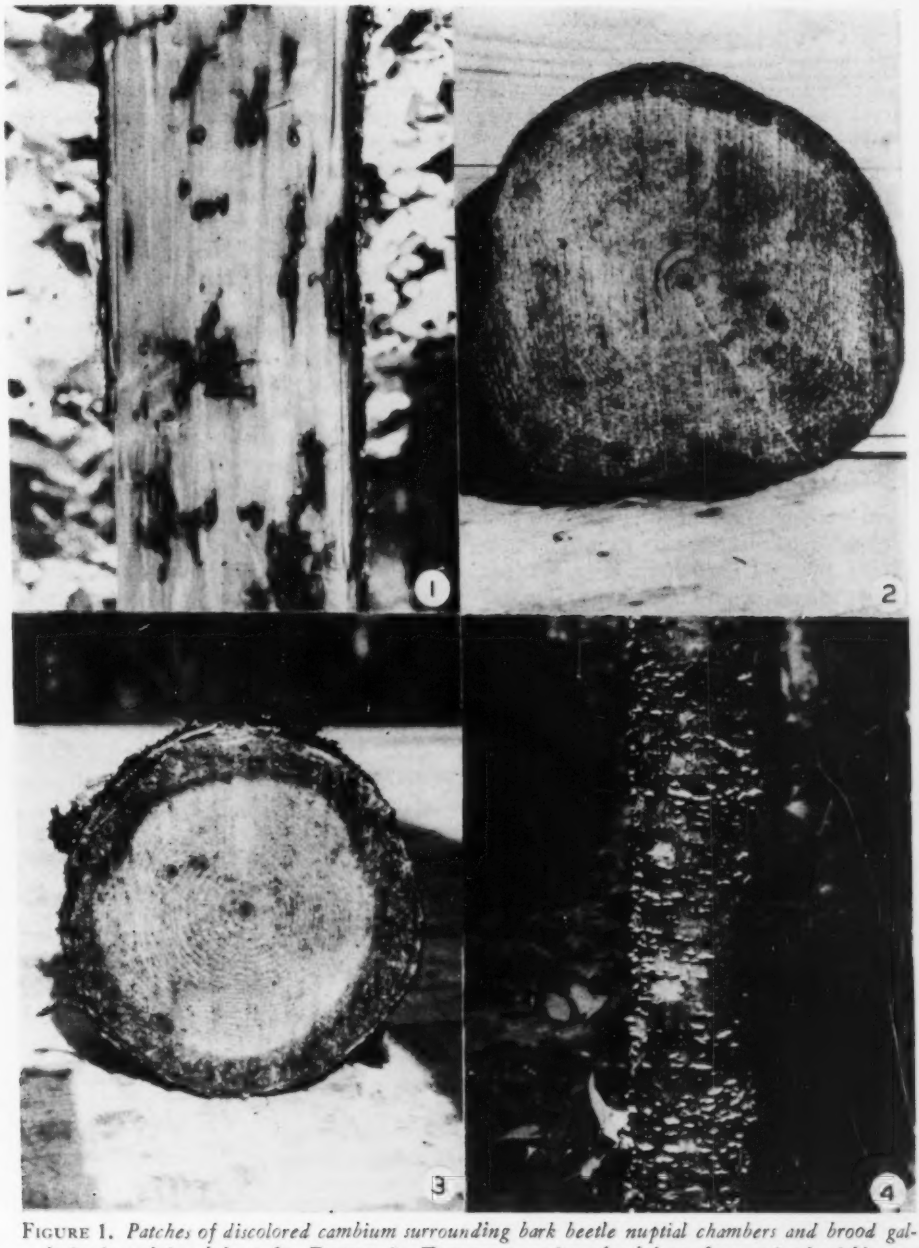

FIGURE 1. *Patches of discolored cambium surrounding bark beetle nuptial chambers and brood galleries in a dying balsam fir.* FIGURE 2. *Transverse section of a balsam fir examined within one year after death, showing yellowish-red sap stain in the sapwood.* FIGURE 3. *Transverse section of a balsam fir examined about three years after death, showing pitted sap rot associated with* Polyporus abietinus. FIGURE 4. Polyporus abietinus *fruiting bodies on the trunk of a dead balsam fir.*

or all of the sapwood. Once this foothold has been gained, these and other fungi advance through the wood in all directions until eventually, as a rule, the entire tree is decayed.

The cambial layer of living balsam fir is pale yellow and is quite moist in the spring and early summer. In areas where some balsam fir mortality had already occurred, trees were almost invariably attacked either shortly before or soon after death by the bark beetle, *Pityokteines sparsus*. The nuptial chambers and brood galleries formed in the cambium by this species were soon surrounded by relatively dry, reddish-brown cambium, although the cambium surrounding the discolored zones remained moist and pale yellow (Fig. 1). Struble (1937) reported a similar condition in white fir and red fir attacked by the fir engraver beetle in the western United States. In about four weeks the brown cambial patches spread until all of the cambium was dry and discolored. Two fungi were consistently isolated from the patches of discolored cambium surrounding bark beetle mines, and from the wood immediately beneath these patches, in dying trees or trees that had recently died (Table 1). These were an Ascomycete, *Ophiostoma bicolor* Davidson and Wells, recently named and described by Davidson (1955), and an unidentified yeast which on malt agar forms slow-growing, pearly-white colonies resembling those of bacteria. Table 1 shows the almost total absence of these fungi in the adjacent pale yellow cambium.

The sapwood and heartwood of balsam fir are practically indistinguishable visually. However, examinations of thin slices of wood consistently revealed that the wood adjacent to the cambium was somewhat wetter and paler than the remainder. This region was generally from ½- to 1-inch wide, depending upon the diameter of the bole. Microscopic plasmolysis tests demonstrated that the ray cells in this region could be plasmolyzed in 0.6M solutions of sodium and calcium chlorides, and deplasmolyzed on the addition of water. Few ray cells were shown to be alive in this way in the drier region. Throughout this paper the term sapwood refers to this outer region, which is usually ½- to 1-inch thick in balsam fir.

A progressive reddening of the sapwood was evident during the first year after death (Fig. 2). Although this yellowish-red wood appeared as firm and hard as sound wood, laboratory tests revealed that its toughness

TABLE 1. The frequency of isolation of different fungi from the cambium and underlying wood of balsam fir that had died recently.

	Cambium		Wood		
Culture determination	Stained areas	Pale yellow	Beneath stained cambium	Beneath pale yellow cambium	Total
Yeast (unidentified)	64	–	17	–	81
Ophiostoma bicolor	50	1	14	–	65
Fungus F	2	–	2	–	4
Stereum chailletii	2	–	3	–	5
Basidiomycetes (unidentified)	2	–	–	–	2
Contaminated	28	5	5	1	39
Sterile	1	38	3	11	53
Total no. cultures	100[1]	44	31[2]	12	187[3]

[1]Forty-nine cultures yielded both yeast and *O. bicolor*.
[2]Thirteen cultures yielded both yeast and *O. bicolor*.
[3]Sixty-two cultures yielded both yeast and *O. bicolor*.

had been significantly reduced and for this reason it is referred to as incipient deterioration (Basham, 1959). Two fungi were consistently associated with this stain; (1) an unidentified fungus referred to as *Fungus F* which has tentatively been placed in the genus *Cephalosporium* of the Fungi Imperfecti by R. F. Cain of the University of Toronto (its perfect stage, when found, probably will belong in the genus *Ophiostoma*) and (2) *Stereum chailletii* Pers., a Basidiomycete recently encountered by others in dead coniferous trees in North America (Davidson and Newell 1953, Engelhardt 1957, Wright *et al.* 1956). Fruiting bodies of the latter fungus were not found during this investigation.

Approximately one year after a tree had died, the discolored sapwood began to soften markedly. One fungus, the Basidiomycete *Polyporus abietinus* (Dicks.) Fr., was consistently isolated from the advanced white pitted sap rot that formed an outer ring of varying depth in all balsam firs examined that had been dead for longer than one year (Fig. 3). From two to five years after tree death, large numbers of fruiting bodies of this fungus were formed on the bark, particularly towards the base of the trunk (Fig. 4).

White pitted sap rot accounted for 92 percent of the volume of advanced sap rot present in the trees examined and brown cubical sap rots for the remainder. Two fungi, *Fomes pinicola* (Swartz) Cookę and *Coniophora puteana* (Schum. ex Fr.) Karst., were consistently isolated from the latter. These brown rots occasionally formed a continuous ring in the outer wood of dead balsam fir, but occurred more frequently as patches in the *P. abietinus* sap rot. Judging from the appearance and position of these rots, it may be assumed that the causal organisms in most cases merely followed *P. abietinus* rot and seldom infected sound wood. Nevertheless, it was noticed that once established, these brown rot fungi were usually able to penetrate faster into the heartwood than *P. abietinus*.

Progress of Deterioration

In assessing deterioration of dead trees in this study, primary consideration has been given to loss of usable wood volume, with particular reference to utilization of balsam fir in the manufacture of pulp. With the probable exception of the sawyer beetles,[3] the activity of insects in the dead trees resulted in little or no direct deterioration in this sense. Belyea (1952a) has pointed out that sawyer beetles complete their penetration of dead trees quickly, and a year or year and a half after death their direct deteriorating effects are complete.

Sap-rotting fungi, on the other hand, actively destroy appreciable volumes of wood, and their effect is progressive over a longer period. Practically all of the 189 dead trees examined revealed some form of fungal deterioration in the outer wood of the stem. Only two trees were without visible deterioration, and these were dissected very soon after apparent death. It was decided that the relationship between four factors and the type and amount of deterioration present in dead balsam fir should be investigated. The four factors are the length of time since death, the season of death, the growth rate during the last years of life, and the type, time, and intensity of insect attack in the dying and dead trees. The effects of these factors will be discussed separately.

Deterioration in relation to the interval since death. The rate of radial penetration of advanced deterioration (sap rot) was approximately the same in the smaller trees as in the larger. Hence, at any given time after death, a greater percentage of the volume of a 6-inch tree would be deteriorated than would that of a 10-inch tree. Such a relationship between tree diameter and percentage of volume deteriorated has been found by other workers (Buchanan and Englerth 1940; Kimmey and Furniss 1943). For this reason, in assessing the

[3]McNeel, W. *Op. Cit.*

TABLE 2. The rate of deterioration of dead balsam fir.

No. years since death	No. trees examined	Total merch. vol.[1]	Average merch. vol. per tree	Total vol. of sap stain	Merch. vol. occupied by sap stain	Total vol. of sap rot	Merch. vol. occupied by sap rot	Corrected merch. vol. occupied by sap rot[2]
		Cu. ft.	*Cu. ft.*	*Cu. ft.*	*Percent*	*Cu. ft.*	*Percent*	*Percent*
0-1	40	239.0	6.0	59.5	24.9	0.6	0.0	0.0
1-2	51	375.7	7.4	48.1	12.8	86.7	23.1	25.0
2-3	57	419.1	7.4	24.4	5.8	138.7	33.1	36.2
3-4	34	173.5	5.1	9.4	5.4	77.4	44.6	40.3
4-5	7	37.9	5.4	1.3	3.4	17.1	45.1	41.9

[1]Volume inside bark, from stump height to a 3-inch top.
[2]To compensate for variations in the diameter class distribution in the five groups of trees. Calculations described in text.

rate of deterioration of dead trees based on the percentage of the volume deteriorated, any marked variation in the d.b.h. class distribution among the groups of trees classified as to interval since death, would be an obvious source of error.

The annual progress of deterioration of the trees examined in this study is summarized in Table 2. It is evident that the trees examined which had been dead for one to three years tended to be larger than the average, whereas those dead for three to five years were generally smaller. This was not because of any effect of tree size on survival, but simply because many of the former trees were located in plots established in stands of larger average diameters than the latter.

A survey of 1,122 dead balsam firs in typical budworm damaged stands in the study region revealed that the five d.b.h. classes, 6, 7, 8, 9, and 10-plus inches, occur in the following percentages: 33.6, 23.6, 18.4, 12.4, and 12.0, respectively. To convert each group of trees to this average d.b.h. class distribution, the total number of trees in each group was multiplied by these percentages. The average total merchantable volume and the average volume of advanced deterioration per tree of trees in each of the five d.b.h. classes were then multiplied by the revised number of trees in each class. From the resultant figures, the percentage of the total merchantable volume occupied by sap rot was determined for trees in each interval since death. In this way the error resulting from differences in the average size of trees in the different groups was removed. It should be pointed out that in no case did the application of this correction alter the percentage deterioration figure for one group of trees by more than 4.3 percent.

Table 2 shows that in trees dead for less than one year there was a negligible amount of sap rot (advanced deterioration). All of the sap rot recorded for this death-year class was found in a single tree. However, most of these trees did possess sap stain, the yellowish-red discoloration in the outer sapwood (incipient deterioration) associated with the presence of *Stereum chailletii* and *Fungus F.*

All but 6 of the 149 trees that had been dead for longer than one year possessed sap rot. The corrected percentages of the total merchantable volume in this state were roughly 25 in trees dead from one to two years, 36 in trees dead two to three years, and 40 and 42 in trees dead three to four and four to five years, respectively. It is interesting to note that for the first three years after death there was a defintie tendency for the sap rot to permeate in any one year that portion of the tree in which sap stain was present the year before.

It is also evident from Table 2 that the rate of deterioration decreased noticeably

after trees had been dead for about three years. Although the average depth of sap stain or sap rot and percentage of merchantable volume deteriorated continued to increase, they did so at a much slower rate. This may be because of a greater decay resistance in the heartwood than the sapwood owing to the presence of growth-inhibiting substances, or to its lower moisture content. However, since the sapwood and heartwood of balsam fir were so difficult to distinguish, no specific data on this point could be collected.

The percentage of the total merchantable volume occupied by heart rot, which was present in the trees before they died, is presented in Table 3. It is evident that there was a tendency for more heart rot to occur in those trees that had been dead for longer periods. Basham (1957) observed a similar, but much more pronounced, relationship in a study of the deterioration of fire-killed pine in Ontario. In both studies, the rate of increase of heart rot was greater than that observed in living trees over a similar period of time, namely, four to five years.

An average of 10.4 percent of the merchantable volume of the 189 trees examined was occupied by heart rot (Table 3). To overcome the variations in the amount of heart rot that were recorded for trees examined at different intervals after death, which may not be significant, 10.4 percent of the total merchantable volume of the trees in each group was classified as heart rot. Taking both heart rot and sap rot into consideration, the reduction in the sound, recoverable portion of the total merchantable volume of these trees, as the interval since death increased, is apparent in Figure 5.

Deterioration in relation to the season of tree death. Gäumann (1930), in an investigation carried out under controlled conditions, concluded that the susceptibility to fungus infection and the destructibility of spruce and fir wood is greatest during the period of most active metabolism, that is, from the commencement of the circulation of the sap until the conclusion of annual ring formation. Other workers have shown that summer storage results in greater amounts of decay in timber left in the open than winter storage, so that summer-felled trees generally deteriorate faster than winter-felled (Boyce 1923, Findlay 1941, Nylinder and Rennerfelt 1954). This is presumably because of the cessation of fungal and insect invasions during the colder months, as well as the lower moisture content and temperature of the wood which results in far less favorable conditions for the growth and spread of established fungi.

The relationship between the average depth of radial penetration of visible sap rot or stain and the season of death of balsam fir is presented in Table 4. Only those trees which were examined from 1 to

TABLE 3. The occurence of heart rot in dead balsam fir.

No. years since death	No. trees examined	Average age	Total merch. vol.[1]	Total vol. of heart rot	Merch. vol. occupied by heart rot
		Years	*Cu. ft.*	*Cu. ft.*	*Percent*
0-1	40	78	239.0	21.8	9.1
1-2	51	87	375.7	33.8	9.0
2-3	57	68	419.1	45.7	10.9
3-4	34	70	173.5	22.7	13.1
4-5	7	89	37.9	5.6	14.9
Total or average	189	77	1245.2	129.6	10.4

[1]Volume inside bark, from stump height to a 3-inch top.

4 years after death, and for which the season of death was known, were included in this table. Trees examined less than one year after death had sap stain only, and this was sometimes faint and difficult to outline. The number of trees examined 4 to 5 years after death was too small to analyze statistically.

Since nearly all of the sectioning was carried out during the months of July and August, in each death-year class the winter-killed trees had been dead for an average of six months longer than the summer-killed trees. Therefore, to compare the depth of radial penetration of sap rot or stain of winter-killed and summer-killed trees at similar intervals since death, it was necessary to adjust the figures obtained from the winter-killed trees. This was done by constructing a curve from the figures representing the average depth of sap rot or stain of the three groups of winter-killed

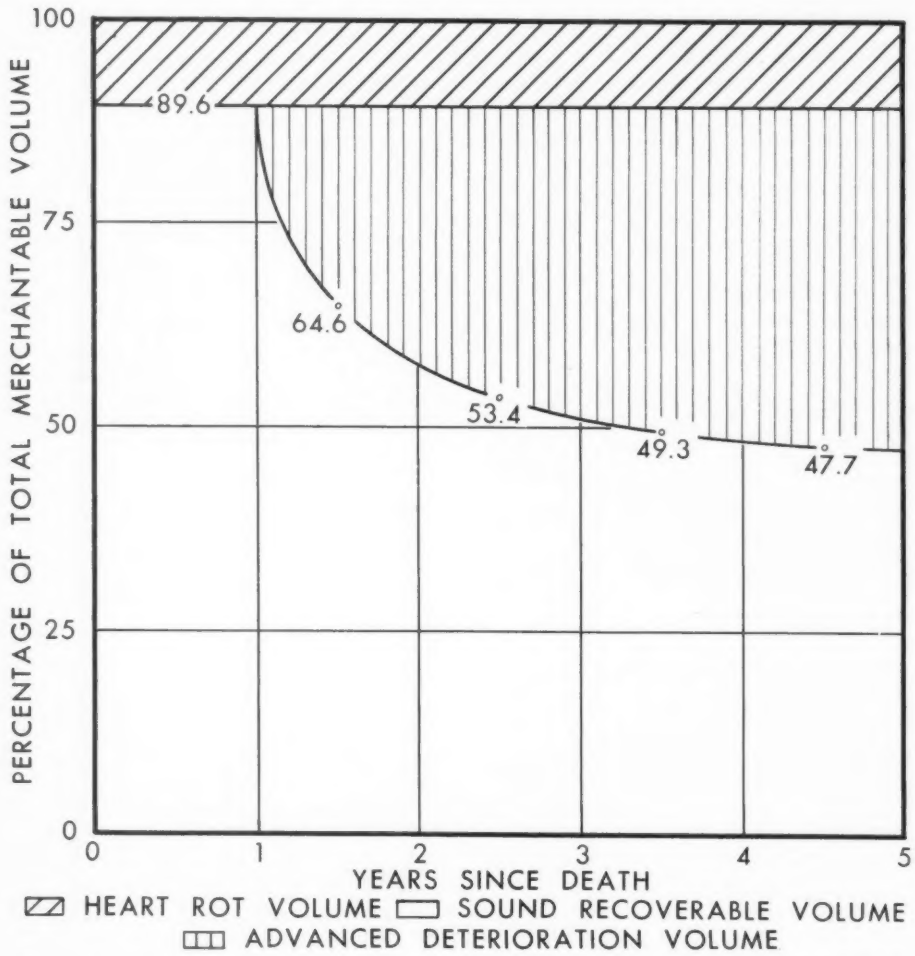

FIGURE 5. *The relation between the sound, recoverable volume of dead balsam fir trees and the interval since death.*

TABLE 4. The relationship between the depth of radial penetration of deteriorated wood and the season of death in killed balsam fir.

Time since death Years	Months	Trees dying during summer (May to September) No. of trees (1)	Average depth of radial penetration of sap rot or stain (inches) (2)	Trees dying during winter (October to April) No. of trees (3)	Average depth of radial penetration of sap rot or stain (inches) (4)	Comparable depth of penetration[1] (inches) (5)	Significance of the difference between the means of the depth of radial penetration of sap rot or stain in summer-killed and winter-killed trees. Degrees of freedom (6)	Value of t (7)	Probability (8)
1-2	12-17	25	0.56			0.51	48	1.52	.14 (not sig.)
	17-24			25	0.52				
2-3	24-29	25	0.68			0.55	48	1.98	.05
	29-36			25	0.59				
3-4	36-41	10	0.94			0.66	18	1.15	.27 (not sig.)
	41-48			10	0.76				

[1]Values interpolated from a curve drawn from column (4).

trees (column 4, Table 4). The average depth of sap rot or stain in these trees at periods since death, corresponding to those at which the summer-killed trees were sampled, were obtained from this curve (column 5, Table 4).

The difference between the means of the depth of radial penetration of sap rot or stain of summer-killed and winter-killed trees examined from 2 to 3 years after death was significant at the 5 percent level of probability, but the differences in the two other death-year groups were not significant (Table 4). Thus, there was a tendency for summer-killed trees to deteriorate more rapidly than those dying in the winter, but this difference was not consistently significant.

Deterioration in relation to tree growth rate. It is generally agreed that fungi penetrate more slowly into wood having close annual rings than into less dense, fast-grown wood (Wagener and Davidson 1954), presumably because of the greater number of cell walls which must be penetrated in the former. Such a relationship was found in fire-killed Douglas-fir by Kimmey and Furniss (1943).

In the present study, an examination was made of the relationship between the radial growth during the last two decades in the life of each tree (including in most cases the part of the tree deteriorated during the first four years after death) and the depth of radial penetration of sap rot or stain. For this purpose trees were grouped together on the basis of season of and interval since death. The average radii at stump height of the last 20 years' growth, and of visible sap rot or stain for each tree, were tabulated. The coefficients of correlation between these two sets of data and the correlation coefficients required for the 5 percent level of significance were calculated for each group of trees (Table 5).

Trees that had been dead for less than one year showed no apparent relationship between depth of visible sap rot or stain (mostly stain) and recent growth rate. Microscopic examinations of the stained sapwood of these trees revealed that *Fungus F* and *Stereum chailletii* passed from cell to cell only through pit apertures and membranes. This probably explains why they were apparently not affected by the spacing of the cell walls. *Polyporus abietinus*, on the other hand, penetrated directly through the cell walls, so that in trees dead for longer than one year a relationship between the depth of penetration and tree growth rate might be expected. Table 5 shows

that a positive relationship did exist in all groups of trees that had been dead for over one year. There exists, then, a tendency for trees with widely spaced annual rings in the sapwood to deteriorate faster than trees with narrowly spaced rings. However, in only one group was this relationship significant at the 5 percent level.

Interrelationships Between Insects and Fungi

The Relation of Insect Activity to Fungal Spread and Infection

Bark beetles. Many studies have demonstrated that several of the fungi, mainly *Ophiostoma* spp., which precede sap-rotting organisms and are responsible for stains in the sapwood of pine and spruce, are associated with specific bark beetles and are transmitted by these insects to dying trees and trees that have recently died (Grosmann 1930, Leach *et al.* 1934, Rumbold 1936, Wright 1938, Verrall 1941). The constant association of certain yeasts with some of these bark beetle-stain fungus relationships has also been demonstrated (Leach *et al.* 1934, Rennerfelt 1950, Rumbold 1941). The fact that *Ophiostoma bicolor* and the yeast were isolated only from discolored cambium adjacent to chambers and galleries formed by the bark beetle, *Pityokteines sparsus*, suggested that this insect might be instrumental in infecting dying balsam firs with these fungi.

Efforts to isolate specific fungi from the external body parts of insect adults or larvae are complicated by the presence of other organisms. Bacteria and other fungi, such as *Penicillium* spp., which play no known role in the deterioration of balsam fir, are carried by most insects. This difficulty was partially overcome by repeatedly washing adults and larvae of *P. sparsus* in hyamine, an organic fungicidal solution, before placing them on malt agar plates. The success of this technique is apparently due either to a difference in the susceptibility of the organisms to the fungicide, or to the fungi being borne in spore pouches or on other protected body parts of the insect (Francke-Grosmann 1956).

The desirability of trapping adult bark beetles in flight to determine whether or not they are carrying *O. bicolor* and the yeast is obvious. This was not attempted, however, because the only simple method of securing these very small insects is by the use of traps, and fungi might then be ac-

TABLE 5. The relationship between the depth of radial penetration of deteriorated wood and tree growth rate during the last 20 years before death in killed balsam fir.

No. years since death	Season of death	No. of trees	Average radial distance at stump height (inches)		Coefficient of correlation r	Correlation coefficient required for 5% level of significance[1]
			Visible sap rot or stain	Last 20 years of growth		
0-1	summer	17	0.38	1.14	−0.068	0.482
0-1	winter	19	0.41	1.04	+0.007	0.456
1-2	summer	21	0.56	1.08	+0.524[2]	0.433
1-2	winter	24	0.53	0.95	+0.169	0.404
2-3	summer	25	0.68	1.07	+0.293	0.396
2-3	winter	19	0.60	0.80	+0.319	0.456
3-4	summer	10	0.94	0.52	+0.183	0.632
3-4	winter	8	0.78	0.63	+0.651	0.707

[1]From Table 5-A, R. A. Fisher, "Statistical Methods for Research Workers."
[2]r significant at the 5 percent level of probability.

quired from other trapped insects. Furthermore, adults were easily obtainable from dying and dead brood trees without risking chance contamination.

Forty-four mature *P. sparsus* adults were removed from several recently attacked, dying trees. *O. bicolor* and the yeast were isolated from approximately 50 percent of the beetles. Since most of the remainder yielded other fungi or bacteria, they may also have carried these two fungi which were suppressed in culture.

Twelve larvae and eight pupae of *P. sparsus* were removed from dead balsam fir, surface sterilized, and plated. Eight of the 12 larvae and three of the eight pupae yielded isolates of *O. bicolor* with the yeast.

Fifty-nine young *P. sparsus* adults which were about to emerge from dead balsam fir were collected. These were also given a partial surface sterilization and plated, and *O. bicolor* and the yeast were again isolated from approximately 50 percent of the beetles.

The bark beetle *P. sparsus* thus appears to carry these two fungi in a viable condition at most, if not all, stages of its life cycle. The spores of most *Ophiostoma* spp. are mucilaginous and not adapted for wind dissemination, and insects are often associated with the spread of such spores. It seemed clear that *P. sparsus* facilitates the entry of *O. bicolor* and the yeast.

To test this theory, healthy balsam fir bolts protected from air-borne spores were subjected to *P. sparsus* attack. Early in June, four healthy balsam fir trees were felled, and from each two 18-inch bolts were cut. The ends of the bolts were immediately coated with "Braco," an asphalt grafting compound, to prevent fungal infection.

The eight bolts were then placed singly in cages sealed with factory cotton (Fig. 6). Tests with sterile agar containers covered only with a single layer of factory cotton had shown that this cloth was an effective spore barrier. Hence, the passage of *P. sparsus* adults and of fungus spores into and out of the cages was prevented without unduly interfering with aeration. At this time there were indications that the early summer flight of *P. sparsus* adults from dead to dying balsam fir had commenced. A large number of young adult beetles which were about to emerge was collected from two balsam fir that had been dead for about one year. Fifty female beetles and 30 males were placed in each cage containing one of each pair of bolts. The remaining four bolts served as controls. The cages were then placed in a small clearing in the forest about 100 feet from the two dead trees from which the beetles had been collected.

When the eight caged balsam fir bolts were removed and examined two months later, it was found that three of the four bolts exposed to adult bark beetles had been heavily attacked. Extensive areas of the cambium were occupied by networks of egg galleries and larval mines. In these areas the cambium was stained a dark reddish-brown color, but the remainder of the cambium was pale yellow. In the fourth bolt that had been exposed to *P. sparsus* adults, egg galleries and larval mines were limited to the cambium near the ends of the bolts, so that the brown stain of the cambium was not as extensive as in the other three beetle-infested bolts.

The bark was removed from the four bolts that had been protected from bark beetle attack. The cambium of all four bolts was pale yellow, with the exception of light brown fringes near the ends of the bolts (Fig. 7).

Bits of discolored and pale yellow cambium were removed aseptically from bolts exposed to the insects and from protected bolts, and placed on malt agar plates. Eight cultures were made from each bolt. Successful isolations of *O. bicolor* and yeast were made from the discolored cambium of each of the four bolts exposed to *P. sparsus* adults, whereas these fungi were not isolated from the protected bolts.

Thus it seems clear that *O. bicolor* and the yeast are carried by *P. sparsus* adults from dead to dying balsam fir trees, and

FIGURE 6. *Cage containing a bolt cut from a sound, living balsam fir.* FIGURE 7. *Two peeled bolts cut from the same healthy balsam fir after removal from cages. The bolt on the left was removed from a cage into which bark beetles had been introduced; that on the right from a cage in which bark beetles had been absent.* FIGURE 8. *Portion of a balsam fir examined two to three years after death, showing a sawyer beetle entrance hole (arrow) and ribbon of sap rot associated with the larval mine.* FIGURE 9. *Transverse section of the balsam fir bolt illustrated in Figure 8.*

deposited in the cambium or outer xylem of the latter while the insects are making their nuptial chambers and brood galleries. From these loci the two fungi spread throughout the cambium and to some extent into the xylem, and are eventually transported by bark beetle adults to other dying trees or trees that have recently died.

Weevils. One of the very few balsam fir trees encountered that had been heavily attacked by the weevil *Pissodes dubius* was felled and three bolts were removed and placed in cages. Nine emerging *P. dubius* adults were selected for testing, and from these, six beaks, ten legs, and six sections of abdominal integument were surface sterilized with hyamine and plated. *O. bicolor* and the yeast were isolated from three of the beaks and six of the legs, indicating that *P. dubius* also may introduce these fungi into the cambium in the process of laying eggs in dying trees.

Sawyer beetles. The two fungi that first extensively invade the sapwood of dead balsam fir, *Fungus F* and *Stereum chailletii*, were consistently isolated from the sapwood of trees that had been dead for periods as short as four to six weeks. In most of these trees the only avenues into the sapwood for airborne spores were the small entrance holes formed through the bark by *P. sparsus*. The fact that fructifications of these fungi were never encountered indicated that there is little inoculum in the forest air. This, coupled with the limited number of avenues of entrance into the sapwood of trees that had recently died, indicated that these fungi might be transmitted from tree to tree in some other manner.

The possibility that insects attacking dying balsam fir or trees that had recently died were responsible for the transmission of *Fungus F* and *S. chailletii* was investigated. These fungi were not isolated from the bark beetle *P. sparsus*. Only one other insect, the sawyer beetle, *Monochamus scutellatus*, heavily attacked nearly every tree examined. The adult beetles emerge from dead trees during the summer months and deposit their eggs in egg slits chewed in the bark of dying trees or trees that have recently died. The hatched larvae bore through the bark and into the wood, usually to a depth of 3 to 4 inches, then return to the outer wood, where they form pupal cells. Belyea (1952a) reported that this process takes from one to two years. The borers then pupate, the adults emerge, and the females lay their eggs in other dying or recently dead trees.

To ascertain whether or not *M. scutellatus* carried spores or hyphae of *Fungus F* or *S. chailletii* in a viable condition from dead to dying balsam fir, adult female borers were hand-caught in flight, killed, and surface sterilized briefly in 95 percent alcohol and 5 percent calcium hypochlorite. They were then dissected, and the mouth parts, antennae, legs, and terminal abdominal sections of the integument were placed on malt agar plates. Eggs were removed from egg slits in the bark of dying trees, and transferred aseptically to malt agar plates.

Despite a high proportion of contaminated or sterile cultures, *Fungus F* was isolated from the mouth parts, legs, and abdomen of *M. scutellatus*, and from the eggs removed from egg slits (Table 6). Hence, *Fungus F* is evidently carried by *M. scutellatus* in flight, and could be introduced by this insect into dying trees or trees that had recently died, either during the chewing of the egg slit by the adult or during actual deposition of the eggs. *Fungus F* was isolated twice from stained cambium and twice from the wood beneath stained cambium of recently dead trees (Table 1). The two trees from which these isolations were made had been dead longer than the others shown in Table 1, and contained numerous Monochamus eggs and larvae. Thus it is possible that this fungus was introduced to these two trees by *M. scutellatus* rather than *P. sparsus*, particularly since *Fungus F* was never isolated from the bodies of the latter insect.

No evidence was found of the method of spread of *Stereum chailletii* from tree to

TABLE 6. The frequency of isolation of different fungi from migrating adult sawyer beetles and their eggs.

Culture determination	Part of insect body cultured					
	Abdomen	Legs	Mouth parts	Antennae	Deposited eggs	Total
Fungus F	2	2	3	--	4	11
Ophiostoma bicolor	--	--	1	1	--	2
Unidentified Fungi Imperfecti	3	1	--	--	--	4
Unidentified Basidiomycete	--	--	1	--	--	1
Contaminated	13	12	4	3	2	34
Sterile	3	2	--	--	10	15
Total no. cultures	21	17	9	4	16	67

tree. The early appearance of this fungus in the deterioration process suggests that it may also be transmitted by bark beetles or sawyer beetles, possibly in the form of conidia or hyphal fragments. This could only be explained by assuming that *S. chailletii* is more sensitive than the yeast, *O. bicolor*, and *Fungus F*, to the surface sterilization treatments used to kill or retard the growth of other fungi and bacteria on the bodies of the insects. The basidiospores of *S. chailletii* are not mucilaginous and therefore not as likely to be dependent upon insect vectors as are those of *Fungus F*. Despite unsuccessful attempts to find fruiting bodies, one cannot ignore the possibility that there may be sufficient air-borne basidiospores of *S. chailletii* in the forest capable of infecting dying or recently dead balsam fir through bark entrance holes made by *P. sparsus* to explain the occurrence of this fungus in the sapwood of trees that have died recently.

The Relation of Sawyer Beetle Activity to Penetration of Sap Rot

Fructifications of *Polyporus abietinus* are very common, and were observed on nearly every coniferous tree or log dead for two to four years. They were almost always encountered on balsam fir trees that had been dead for three or more years. It is safe to assume, therefore, that an abundance of spores of *P. abietinus* are in the forest air throughout most of the growing season. Dead balsam fir trees, even those dead for less than one year, invariably have numerous openings through the bark, resulting mainly from attacks by *P.sparsus*, and, to a less extent, *M. scutellatus*. Hence *P. abietinus* spores can gain entrance through these openings to the sapwood of balsam fir that have recently died, although extensive colonization of the sapwood apparently does not occur until trees have been dead for approximately one year.

Cross sections of several dead trees revealed thin ribbons of *P. abietinus* sap rot extending into the sound heartwood. The ribbons were usually semicircular and attached to the outer band of sap rot at two places. In all cases these were found to be vertical extensions of rot originating from tunnels formed by sawyer beetle larvae (Figs. 8 and 9). Leach *et al.* (1937) found a similar pattern in the development of sap rot caused by *Peniophora gigantea* (Fr.) Massee and the Monochamus population in felled Norway (red) pine logs.

Twenty-four Monochamus larvae found in six trees were removed from their larval mines, surface sterilized, and plated. One isolation of *Ophiostoma bicolor* and one of an unidentified Basidiomycete were obtained, the remainder yielded other fungi or were contaminated. It is unlikely that *P. abietinus* was carried by these larvae, since the six host trees had been dead for less than one year. The possibility exists that the fungus was present on the larval bodies but was completely retarded or

TABLE 7. The relationship between the depth of penetration of deteriorated wood and the density of sawyer beetle holes in killed balsam fir.

Years since death	Season of death	Study blocks examined (number)	Average depth of radial penetration of sap rot or stain (inches)	Average density of sawyer beetle holes[3]	Coefficient of correlation *r*	Value of *t*	Probability
1-2	summer	107	0.42	2.79	+0.250[4]	2.69	0.01
1-2	winter[1]	34	0.47	1.55	+0.481[4]	3.08	<0.01
1-2	winter[2]	104	0.46	3.49	+0.374[4]	4.00	<0.01
2-3	summer	129	0.62	7.10	+0.311[4]	3.66	<0.01
2-3	winter[1]	21	0.47	4.15	+0.213	0.92	0.35
2-3	winter[2]	88	0.55	5.15	+0.279[4]	2.69	<0.01

[1]Trees died without a previous late summer sawyer beetle attack.
[2]Trees died following a late summer sawyer beetle attack.
[3]The number of holes per square foot of wood surface.
[4]*r* significant at the 1 percent level of probability.

killed by the surface sterilization treatment. However, it seems more likely that following the departure of *Monochamus* spp. from the tree, the wind-blown infection spores of *P. abietinus* were carried into the deep recesses of the tunnels, where they germinated and eventually resulted in the ribbons of rot.

Data from the 1-foot blocks cut from trees that had been dead for one to three years were analyzed to find if any relationship existed between the density of sawyer beetle entrance holes and the rate of radial penetration of sap rot or stain. Blocks from trees that had been dead less than one year were not included because it was observed that Monochamus had no apparent effect on the incipient deterioration of these trees. Blocks from trees that had been dead for more than three years were also omitted because by this time any effects of the long-departed insect had disappeared.

In trees dead for one to three years, a definite relationship existed between the density of sawyer beetle attack and the depth of radial penetration of sap rot or stain, with significant positive correlations in five of the six groups of blocks (Table 7). Blocks from trees dead for two to three years and dying in the winter without a previous late summer Monochamus attack, yielded a positive, but not significant, correlation.

It was thought that if *Monochamus* spp. do play an active role in the rate of penetration of deteriorating fungi in these dead balsam firs, trees dying in the winter following late summer sawyer beetle attacks would deteriorate faster than those dying at the same time but with their initial Monochamus attack occurring during the summer following death. Table 8 reveals that the former trees showed a marked increase in the percentage of their total mer-

TABLE 8. The effect of late summer sawyer beetle attacks on the rate of deterioration of winter-killed balsam fir trees.

Years since death	No. of trees	Total merch. volume occupied by sap rot[1] (percent)
NO PREVIOUS LATE SUMMER ATTACK		
1-2	7	24.9
2-3	9	25.6
3-4	6	29.1
WITH PREVIOUS LATE SUMMER ATTACK		
1-2	18	22.0
2-3	16	35.9
3-4	4	43.3

[1]Adjusted to compensate for variations in the diameter class distribution between groups of trees.

chantable volume deteriorated; from 22 percent one to two years after death, to 36 percent two to three years after death, and finally to 43 percent three to four years after death. Trees dying in the winter without previous late summer sawyer beetle attacks, on the other hand, showed a relatively small increase in the percentage of the total merchantable volume deteriorated over a similar period.

From the above evidence it is concluded that the time and intensity of attack by sawyer beetles have a direct bearing upon the rate of radial penetration of sap rot and stain in balsam fir trees that have died following spruce budworm defoliation.

Summary and Conclusions

This investigation dealt with the fungal and insect deterioration of the merchantable portions, that is, between stump height and a 3-inch top, of balsam fir dying following spruce budworm defoliation. It was discovered that ten insect species and at least five species of fungi habitually invade the merchantable boles of these trees, altering them in such a way that they become progressively less suitable for utilization. The general pattern of deterioration consisted of a relatively sudden invasion by the insects at or near the time of apparent tree death, and a more gradual fungal invasion which, after two years, completely replaced the insects. Evidence has been assembled which indicates that bark beetles, sawyer beetles, and weevils transport certain deteriorating fungi from dead balsam fir to dying trees or trees that have recently died, and that the development of sap rot is related to sawyer beetle activity. Hence, a very close interrelationship was found to exist between the deteriorating insects and fungi.

The conclusion that insects apparently aid in the establishment and penetration of deteriorating fungi in balsam fir dying or dead following spruce budworm defoliation, focuses attention upon the influence of the size of the various insect populations on the rate of pathological deterioration of these trees. In general, these populations vary considerably in different forest regions, depending mainly upon the presence or absence of suitable breeding material. Thus, Kimmey and Furniss (1943), in a study of the deterioration of fire-killed Douglas-fir, found that in undisturbed forests these populations were quite low, and that the amount of borer damage was correlated with the nearness of old burns.

It may be postulated, then, that in the case of the first trees to die in otherwise undisturbed forests, the rate of tree deterioration as a rule would be slower than that in widespread infestations where some mortality had already occurred. A comparison of trees that had died recently in the extensive Lake Nipigon infestation and in the much more confined Sibley Peninsula outbreak roughly 40 miles to the south supports this theory. In the latter region, the first trees dying following spruce budworm defoliation were observed to be apparently free of bark beetle attacks and showed no signs of preliminarmy fungal deterioration. This was in sharp contrast to the condition of trees described in this report that had died recently in the Lake Nipigon region.

The task of salvaging extensive areas of dead timber is generally a formidable one, and the disadvantages that inevitably confront the operator may constitute insuperable obstacles to profitable operations. The intensity of insect attack and the rate at which fungal deterioration progresses will influence the period in which economical salvage is possible. It is axiomatic that the more knowledge available concerning the nature, causes, and rate of deterioration of these trees, the easier the formulation of intelligent, workable salvage plans. The reduction in quantity and value of the timber at different intervals following the death of the trees should be estimated as accurately as possible in order that these plans will ensure that the maximum amount of wood is salvaged in the most profitable manner.

This investigation has provided evidence

that sawyer beetles are the only insects that might alter the wood of these trees sufficiently to affect the production of pulp. The extent to which these insects are capable of damaging the wood is limited. Fungal deterioration is therefore primarily responsible for the reluctance of most mills to utilize dead trees. The soft, punky sap rot encountered in all trees dead longer than one year results in water delivery losses and in wood-room losses in the barking, chipping, and screening processes. Decayed wood used in the production of pulp lowers the quality of the product, and resultant reductions in yield of as high as 15.8 percent have been recorded (Baxter, 1943). Balsam fir salvaged within one year after death will produce pulp with very little reduction in yield or quality. If left longer, an appreciable amount of sap rot is encountered, resulting in substantial reductions in the yield and quality of pulp. Woodroom losses may be so great that the yield, calculated on the original rough cord, becomes unprofitable. It is clear that when balsam fir have been dead for longer than one year, their high proportion of rotted wood will constitute an additional hazard for any salvage operation.

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